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VOL. 20, NO. 1 March, 1945

THE QUARTERLY REVIEW
of BIOLOGY

CURRENT STATUS OF OUR KNOWLEDGE OF THE GOLGI APPARATUS IN THE ANIMAL CELL

By HOPE HIBBARD
Oberlin College

INTRODUCTION

THERE have been several summaries of work on the Golgi apparatus of recent date, notably that of Kirkman and Severinghaus (1938), that of Hirsch (1939a) and that of Bourne (1942). They present somewhat different points of view, and this, together with the fact that a number of highly important papers have since been published, suggests this additional review.

Prior to the time of the publication of the paper by Golgi from which stems the enormous volume of literature on the subject, there were at least ten papers in which mention or figures of cellular components were included that many later investigators have thought might have been called Golgi apparatus had the papers appeared at later dates. From Golgi's publication in 1898 to the present time somewhat over two thousand descriptions and interpretations of this structure have appeared. Golgi himself lived for many years in scientific seclusion, and one wonders what his thoughts may have been regarding all the furor of discussion of the structures bearing his name.

An analysis of the numbers of papers appearing year by year shows a slow increase in interest in the subject for the first twenty years, then, beginning in 1920, a sharper increase reaching a peak in 1928–30, followed by a sharp decrease to the present. Some of the most recent falling off of publication must be ascribed to war conditions, primarily because research is not going on as in peace time and also because many foreign papers are not available. But the trend of decreasing numbers of papers year by year was well started before the outbreak of the present war. A graphic summary of these data may be seen in figure 1. The titles counted before 1938 correspond for the most part to those listed in the extremely full bibliography included in the book by Hirsch. The list includes a few papers on plant cytology, but no effort has been made to search the botanical literature.

During the first half of the period from the discovery of the Golgi apparatus to the present, investigators were primarily concerned with morphological descriptions of it in all sorts of cell types. Just before and during the peak years some of the very active workers were Beams, Bowen, Gatenby, Guilliermond, Hirschler, Ludford, Nassonov, and Parat,—names which students of cytology will recognize as catalysing agents in this type of research. Through these peak years, and since, questions as to the nature of the apparatus and its physiological significance have been uppermost. Does the falling off in the number of papers indicate an increasing lack of interest, or the general acceptance of a solution? May we expect that the curve will fall entirely and that this problem will retire into the limbo of history as one of the amazing phenomena in the annals of controversial scientific literature?

It is necessary at the outset to admit that there does not seem to be much agreement as to the nature and functioning of the Golgi apparatus. To quote from MacLennan (1939) as to the situation in Protozoa, "The term Golgi body, being based upon non-specific criteria . . . includes a heterogeneous group of structures, including scattered endoplasmic granules and granules associated with contractile vacuoles or fused to form heavy and permanent vacuolar membranes. . . . Since the impregnation reactions themselves do not reveal homologies which must be based on composition and function, the retention of the term Golgi body is merely a convenience to bridge the change from reliance on the non-specific osmic techniques to reliance upon cytochemical and physiological criteria." There is the crux of the matter. In all the years during which cytologists have been discussing the Golgi apparatus, the basic criterion of identification has been impregnation with osmic acid or silver nitrate, neither of which is specific.

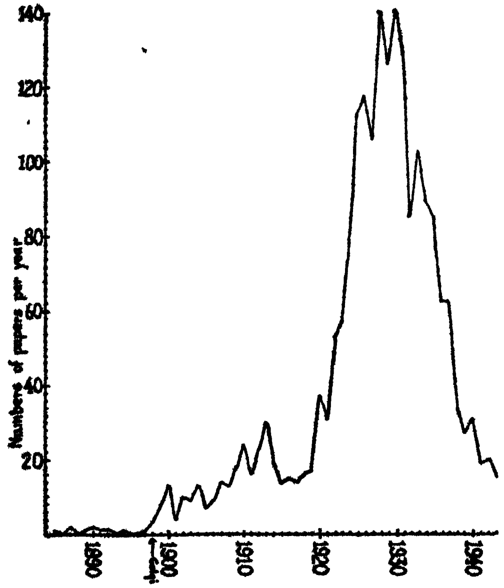

FIG. 1. GRAPH SHOWING DISTRIBUTION OF PAPERS ON THE GOLGI APPARATUS OVER THE YEARS
2074 titles are represented

The picture is complicated for the general reader by the abundance of terms used by individual workers for slight variations in observed details. The tendency to coin new names did not stop with early workers using a new technique to demonstrate something hitherto overlooked, but it continues down to the present. Thus Hirsch (1939a) is able to list in a table with dates, authors, and definitions, one hundred and twenty names for all or for parts of the Golgi apparatus. And Hirsch attempts to re-interpret all these names in terms of his own particular categories. On the other hand, Salazar (1942) has translated Hirsch's names as well as many previously invented by earlier workers into "Golgi apparatus" and "para-Golgi apparatus"; and so on.

Some of the questions most frequently asked as to the Golgi apparatus are: (1) Does it exist as figured or is it an artefact? (2) Is it a permanent structure or does it sometimes disappear? (3) Is its form significant? (4) What are its physical characteristics? (5) What is it, chemically speaking? (6) What are its functions? These questions will be discussed, in the light of what has been published during the last six years, in the following sections.

ARTEFACT?

Probably no cytologist who ever worked upon this problem would deny the existence of something special that blackens with osmic acid and silver nitrate. It is quite obvious that the entire cell does not blacken uniformly. The suggestion of an artefact implies only a possible displacement of materials in the living cell during the preparation for examination, or changes in form, so that the resulting "apparatus" is somewhat different from the special materials or structures that were present in the living and functioning cell at first. Worley and Worley (1943) and Worley (1943b) demonstrated the high susceptibility of cytoplasmic inclusions to changes in form or displacement or both, in embryonic and larval cells of nudibranch molluscs, when there is variation in hydrostatic pressure, as in drying or during fixation. Thus vesicles may be ruptured, and their contents may spring to the surfaces of nearby fatty or albuminous yolk, or may form batonnets in the cytoplasm. Moreover, both intact and ruptured vesicles may be seen in the same living cell, a fact which might lead to erroneous descriptions of more than one type of cytoplasmic inclusion in fixed material. Worley and Worley assume that these vesicles are the Golgi apparatus. They appear as granules, droplets, vesicles, or masses when alive; after fixation artefacts may appear as rings, plates, cups, discs, etc. Similar form changes may be simulated in fresh material by creating shrinkage, comparable to that produced by fixatives, with hypertonic salt solutions.

At an earlier date, Carter (1928) described in the veliger of the nudibranch, *Aeolidia*, a variety of granules in the living cells and among them many with Janus green stained crescents attached.

Figure 19 by Worley (1944a) and figure 7 by Carter (1928) show almost identical bodies, —Golgi bodies, according to Worley, and reserve food vacuoles with mitochondria attached, according to Carter.

Direct proof of the fidelity of the fixed picture by observation of the structure in the same form in the living cell has not been accomplished generally. Although Kirkman and Severinghaus state that "the time-honored belief that Golgi materials cannot be seen in living cells is no longer pertinent," a statement with which Hirsch (1939) is in agreement, they cast doubt on the identity of much that has been described as Golgi material in living cells, such as vacuoles or fat globules. While Hirsch claims agreement with the statement of Kirkman and Severinghaus, he admits that he is unable to see the Golgi substance in the Golgi field in unstained preparations of gland cells. Since Hirsch is responsible for much painstaking and accurate preparation and observation of the living pancreas cell in the mouse, where he kept the circulation about the acinus intact during the whole period of observation and did not in any way dissociate the cells, his failure to see a network in that area where he could impregnate it constitutes an important observation. The writer was unable to see in the living proventriculus or gizzard of the chick anything resembling the enormous and easily demonstrated black apparatus of appropriately fixed tissues. This has been the experience of most cytologists in attempting to discern the typical network in somatic cells of vertebrates.

Although the authors quoted above doubted the correctness of interpreting things like fat droplets or vacuoles as Golgi bodies, they assumed as a matter of course that the Golgi bodies in male germ cells are correctly identified and named. These, unlike those in Hirsch's gland cells, are clearly visible alive, both unstained and stained vitally by Janus green, and from observations of this sort comes most of the evidence that the Golgi apparatus may be seen in living cells. Filhol (1938), it is true, found similar bodies which were visible in all living unstained cells observed in many parts of the reproductive apparatus of pulmonates, bodies which also stained with Janus green. His interpretation of these will be discussed further on (p. 4). These differences alone would seem to cast some doubt on the identity of the Golgi networks and the discrete dictyosomes found in male germ cells. Kirkman and Severinghaus (1938), however, conclude that the latter are actually Golgi material like that of the somatic cells, as follows: "This evidence" [the secretion of the acrosome by Golgi bodies] "is so clear-cut in many instances that the only way of getting around it is by claiming, with the upholders of the vacuome hypothesis, that the dictyosomes of male germ cells do not represent Golgi material, but, as stated by Wilson and Pollister (1937) this claim can no longer be supported in the face of conclusive evidence that 'there is no substantial difference between the Golgi bodies of the germ cells and those of other tissue cells'" (pp. 85, 86). It may be noted that the phrase quoted from Wilson and Pollister is taken from a complete sentence which is qualified as follows: "The observation of their film-like, frequently cup-like, shape is in agreement with the findings of many other cytologists, not only in the germ cells but also in the tissue cells, and *in this respect* the findings on *Centrurus* and *Centruroides* support the contention that there is no substantial difference between the Golgi bodies or the germ cells and those of other tissue cells." (pp. 415, 416, italics mine.) The phrase in its context is far less dogmatic than would appear from the first quotation.

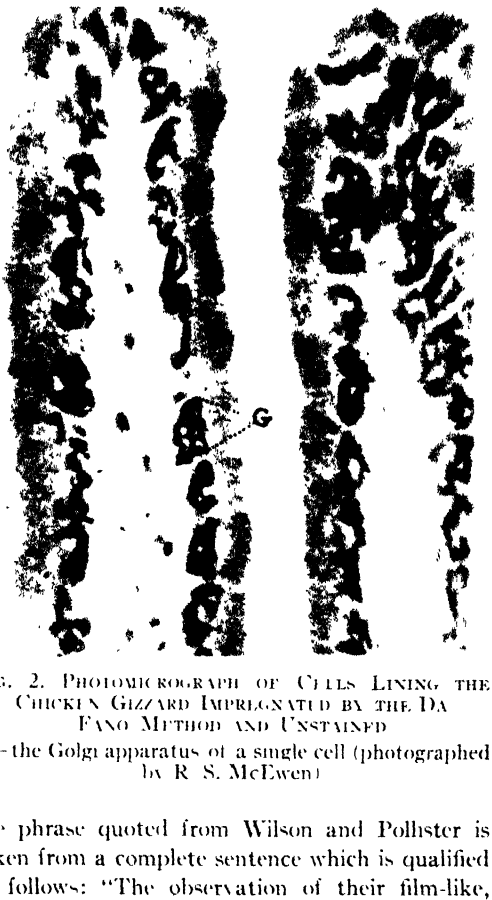

FIG. 2. PHOTOMICROGRAPH OF CELLS LINING THE CHICKEN GIZZARD IMPREGNATED BY THE DA FANO METHOD AND UNSTAINED
G—the Golgi apparatus of a single cell (photographed by R. S. McEwen)

It is quite true that most cytologists currently publishing tacitly assume the dictyosome to be intrinsically the same as any other Golgi apparatus, and they tend to generalize any observation of a special case. Thus the Golgi apparatus, in a broad sense, is assumed to be largely lipoidal because the dictyosomes are lipoidal, or it is said that the Golgi apparatus can be seen in normal living cells primarily because the dictyosome may be seen under those conditions, etc. In Hirsch's various extensive publications such tacit assumptions are evident, and he refers to the Golgi system in the male germ cell as an excellent example of a "mono-system" (see p 7).

While this review is primarily concerned with current ideas and the publications of the last six years, the discussion of the dictyosome cannot be concluded without a reference to the work of Parat (1938), published a year before his death. Though few cytologists have ever supported his interpretation of this problem, the dilemma which he pointed out is still evident in current findings. The facts that the dictyosomes have so frequently been observed in living cells, while the network in somatic cells has not, that they stain with Janus green in the one case but not in the other, that the dictyosomes have been stained with Sudan III, indicating their high lipoid content and that they are stainable with hematoxylin or acid fuchsin while the network is not [though Bachman (1939) described in the guinea pig adrenal cortex an extensive hematoxylin-staining body, after Bouin fixation, which suggests a Golgi net, but which bears no resemblance in form or position to the Golgi apparatus described by Bennett (1940) in the cat]; that the dictyosomes have a more constant morphology than the net and are less deformed by centrifuging;– all these differences must be weighed against the morphological evidence for a similar relation to secretory activity and the fact that both may be blackened by osmic acid. Parat concluded from such comparisons that the dictyosomes had much more in common with chondriosomes than with the heavily blackened masses in gland cells, for instance, and there are several recent publications in which strong reliance is placed upon his conclusions, in work upon other than germ cells. Among them are Filhol and Garrault (1938) on nidamental glands, Feyel (1939) on the guinea pig hypophysis, Dehorne (1938, 1939) on parapodial glands in annelids, where typical filamentous mitochondria were observed to become pachynetic and grow into the duplex Golgi bodies. Also Filhol (1938), in an important series of papers published posthumously, found, by comparing the same adult organs in the complicated reproductive apparatus of thirty species of pulmonates, all transitional conditions from ordinary filamentous mitochondria to dictyosomes closely similar to those described in male germ cells. Moreover, in those species whose cells contain characteristic dictyosomes, during embryological development, the mitochondrial granules swell, then burst, to form the scales or dictyosomes, a name coined by Peroncito for the bodies in male germ cells, but used by many cytologists for similar bodies wherever found. This same process was even observed, in some species, during secretory cycles in adult animals. Ito (1941) found osmic-impregnated Golgi bodies in human spermatogonia in exactly that region of the cell where mitochondria could be demonstrated by other methods All these observations argue against the universal acceptance of the identity of all types of Golgi apparatus.

Indirect proof that the form of the Golgi apparatus seen in fixed tissues exists in the living cell is deduced by Kirkman and Severinghaus (1938) from the fact that the Golgi apparatus behaves characteristically under varying physiological conditions and that it can be centrifuged and segregated from other cytoplasmic constituents. Is it quibbling to suggest that possibly fat droplets or vacuolar constituents or specially constituted regions of cytoplasm, perhaps rich in diffuse lipoids or such other substances as vitamin C, any of which might be responsible for the configurations resulting after impregnation, might vary in position during metabolism or during the application of high centrifugal force? Without asserting this to be the case, it seems to the writer that such "indirect proof" as that advanced by Kirkman and Severinghaus and others proves no more than the original impregnations.

Although Ludford in 1935 published a photomicrograph of such an apparatus in a living fibroblast cell which simply showed an irregular zone of clear cytoplasm not filled by bright granules or mitochondrial granules or vesicles, he stated as late as 1942 that it becomes visible only in degenerating cells or in cells stained with methylene blue. In his own words: "Under no other condition has any structure resembling the Golgi apparatus been seen in living cells in tissue cultures." It is, however, visible in both normal and malignant cells in culture media, after impregnation, according to the same author. This would seem to indicate that the normal protoplasm must be altered, either by degeneration or by staining, before the apparatus can be detected. Warren Lewis has never seen anything resembling a classic Golgi apparatus in a living tissue culture cell (personal communication, 1944).

With regard to artefacts in cytology, Salazar (1942) says, "Demander une 'réalité essentielle' c'est faire une demande prehistorique" because everything one sees is artefact in the sense of metaphysical invariants.

PERMANENCE

Since all must agree that there is some basic reason, or reasons, for the invariable blackening with osmic acid or silver nitrate of certain parts of cells, the other questions enumerated in the Introduction become pertinent. As to the permanence of the apparatus, there is little new evidence to offer from the current literature. In the summary by Kirkman and Severinghaus, numerous authors are quoted who believe it to be a permanent cell structure as well as a few who suggest an origin de novo from nucleus or mitochondria or from the cytoplasm, but they leave the question open, pending further studies on early embryological development. They dismissed the observations of Parat regarding the origin of the Golgi apparatus in various embryonic cells with the statement that he followed the vacuome and not the Golgi apparatus through from egg to germ layer stages; yet it must be remembered that he used the same impregnation techniques that all cytologists use for the demonstration of this apparatus, and that no other Golgi apparatus was in evidence in the stages described. Worley and Worley (1943) traced vesicles which they called Golgi bodies from the mollusc egg into the veliger larva. The Golgi bodies described by them are identified by an unusual method. While these as well as the mitochondria may be stained with acid fuchsin, crystal violet, or iron hematoxylin in fixed preparations, those bodies which appear navy blue after methylene blue vital staining are called Golgi bodies whereas those that are pale blue-green are mitochondria. Worley (1944) found that in *Mytilus* they are also black after osmic acid. It may be remarked that Golgi bodies in general,—in gland cells, for instance—do not stain with acid fuchsin, crystal violet, or iron hematoxylin. However, the Golgi bodies, as identified by Worley, are observed to form fat or yolk or both, in the ovary, and in the embryo and larva as well. Since they continue to synthesize over and over, they appear to be permanent.

Gresson (1940b) observed that Golgi material was introduced into the egg of the mouse by the middle piece of the sperm, and from there it fragmented and was distributed throughout the cytoplasm of the fertilized egg.

Most observers have not been concerned with the first origins of the Golgi apparatus but have started with a well-formed structure and followed its continuity through various subsequent phases. Thus Andrew (1939) followed, in nerve cells of mice from 41 to 733 days old, a gradual fragmentation and final dispersion through the cytoplasm of bodies made visible by the DaFano method. They exhibited no cyclic changes with functional activity of the cells. Stein, Caldwell and Peters (1942) reported that in the anterior pituitary of the mouse there is a decrease in size of the Golgi apparatus, in all but the basophile cells, as the animal ages.

Hibbard (1942) observed changes during the development of the gizzard and proventriculus of the chick. d'Angelo and Charipper (1939) followed the Golgi apparatus of the thyroid during metamorphosis in *Rana pipiens* and observed an originally small compact mass at the apical pole of the nucleus growing into a more distinct network as the hind limb becomes 3 mm. long, becoming a compact mass of twisted rods when it is 18 mm. long, forming rings or nuclear caps when the fore limbs emerge, and forming greatly hypertrophied strands during tail resorption. In a more recent paper, d'Angelo (1941) attempted to correlate these findings with observations on the pituitary, but, while he concluded from changes in the cell types that the thyrotropic hormone is secreted by the basophiles, the pattern of the Golgi apparatus was not clear, and the conclusion was not based upon this structure. Wallraff (1939) followed the Golgi apparatus during the early development of the hypophysis in man.

The descriptions of germ cell changes during the passage of time, already numerous, include additions by Das (1939) on the oogenesis in Rhipcephalus, by Beams and Sheehan (1941) on human oogenesis, by Sluiter (1940) on that in the hen, and by Bhattacharya and Lal (1939) in a summary of oogenesis in general. Guthrie and Jeffers (1938), in a careful study of the ovary in two species of bats, report finding no Golgi apparatus as such, but only fat droplets that occupy the regions where

Golgi bodies are frequently described and which have the configuration of Golgi bodies. Papers by Sato (1940), Richter (1940), McCroan (1940), Mahoney (1940), Ito (1941), Chatton and Tuzet (1941), Rathnavathy (1941) and Gatenby and Collery (1943) describe the transformation of Golgi bodies during spermatogenesis in various animals.

Hirsch (1939a) thinks that the apparatus is permanent in some form in polyphasic secreting cells with recurring cycles, but that it may be lost from monophasic cells at the end of the single secretion synthesis. Since in the latter case the cell itself cannot work over again, the loss is immaterial.

FORM

As to the significance of the form of the Golgi apparatus, I quote from a review by Baker (1942). He speaks of the "casuistical arguments as to whether a given object—rendered visible by incomprehensible methods—is, or is not, to be regarded as a veritable Golgi body. No one knows what structure the ideal technique should show. The Golgi network is often spoken of but it may be queried whether this is often a good description. If such a thing could be constructed as a true model of the complex, magnified several thousand times, and if this model were shown to a member of the general public, it is possible that he would compare it to accumulations (or rows) of spheres embedded in a slimy looking material, or to spheres with bananas adjacent to them or touching their surfaces, or to spheres with separate strings intertwined among them, or even in some cases—if one may dare to suggest a heresy—simply to spheres; but the writer is doubtful whether the word network would often be used to describe the model, though it might occasionally be applicable." Simpson (1941) describes it simply as a twisted intra-cytoplasmic canal of uniform bore and filled with fluid. Bourne (1942) concludes that the apparatus is something which is constantly changing in form and therefore in fixed material presents whatever aspect it happened to have at the moment of fixation. And Salazar, to go back to 1936, wrote, "C'est comme la pluie qui tombe; elle forme un dessin de lignes qui rayent l'atmosphère, mais elle n'est qu'une série de gouttes qui se forment, puis tombent . . . ; l'appareil de Golgi des morphologistes c'est le schéma connu avec lequel des dessinateurs répresent la chose . . . "

While it has been stated that most of the work published during the first quarter century of study of this body was descriptive of its morphology alone, it must also be admitted that morphological aspects continue to play the major role in the more recent attempts to correlate the apparatus with physiological processes. The question as to the significance of its form continues to pose itself. Severinghaus was able to identify the acidophilic and basophilic cells in the hypophysis of the rat on the basis of the form of the Golgi apparatus alone. Poris (1941) also found the apparatus in reptiles to be more compact in acidophiles than in basophiles, though its location in the cytoplasm was variable. On the other hand Copeland (1943), in *Triturus*; Aplington (1942), in *Necturus*; Payne (1942), in the fowl; and Ayres (1941), in the immature rat, found no identifying differences in the Golgi apparatus of hypophysis cell types.

Several authors are so convinced of the validity of its morphology as to base functional interpretations on the observed forms. Thus Baillif (1941) uses the Golgi configuration as an indication of phagocytic response in the rat omentum; Welch and Brodus (1940) found it a delicate method of estimating cellular function in the human thyroid. They interpreted cases of adenomatous goitre, not diagnosed as hyperthyroids, as mild cases of hyperthyroidism notwithstanding the diagnosis, solely because some of them had the marked hypertrophy of the Golgi apparatus found characteristically in exophthalmic goitre. Dalton and Edwards (1942a) found it to be of value in diagnosing mouse neoplasms; but Rauramo and Turpeinen (1940) found a Golgi apparatus in only about half of the seventeen uterine carcinomas studied. Krichesky and Mandel (1943) made careful measurements of cell size and the size of the Golgi apparatus in the uterine glands of the rabbit during pregnancy, and concluded from their results that our ideas of the function of the uterine secretion should be modified. Before the free blastodiscs become implanted the secretion is assumed to act as a nutritive agent, and when the uterine muscles are contracting vigorously the secretion could provide lubrication, but since they found little correlation between the dispersion of the Golgi apparatus and the occasions when an increased secretion would be useful, Krichesky and Mandel conclude that the secretion is not increased at these times and therefore cannot have the functions ascribed to it. They suggest no doubt of the validity of using the morphology of the Golgi apparatus as a measure of secretory activity. Seshacher (1942) used the Golgi apparatus to identify oocytes developing from primordial germ cells in male Apoda and distinguish them from primitive spermatogonia.

In view of the large number of papers by Hirsch and his co-workers, including the Protoplasma Monograph (1939a), which have appeared since the summary by Kirkman and Severinghaus, the morphological data the former have accumulated and their interpretations of it must be discussed. They have examined many types of cells directly, and Hirsch has gone further and re-interpreted the observations of other cytologists in terms of a basic pattern which fits all cases. According to this pattern, there is in each cell a primordial "presubstance" which is homogeneous, though not necessarily a single chemical compound. It often stains with neutral red, usually blackens with silver nitrate and osmic acid. Its origin is shrouded in mystery, awaiting proof as to whether it arises from the cytoplasm directly, or the nucleus, or the mitochondria, or from an interaction of some or all of these. It may appear in the form of droplets, a beaded string, an irregular mass (possibly only when over-impregnated, so as to conceal its true form), elongated threads, or a network. During cellular differentiation or cellular functioning this primordial presubstance develops into the "Golgi system," which is a duplex affair composed of osmiophilic and osmiophobic parts, or Golgi-externum and Golgi-internum. The internum is what Salazar calls the "para-Golgi apparatus." (See 1942 and earlier papers.) In the production of the internum, the cytoplasm with its mitochondria undoubtedly plays some part, though it is not demonstrable morphologically in most cases. Hirsch lists twenty-five cases of vertebrate cells and twenty-one among invertebrates which exhibit this duplex character. Turner (1940) found duplex bodies in Protozoa; Filhol (1938), in his pulmonate material, was always able to see a duplex composition in the impregnated tissues; Dornesco (1938) concluded from extremely careful studies that, in the rat and guinea pig nerve cells, the networks often described were the result of seeing overlapping but discrete dictyosomes. The Golgi-internum, according to the Hirsch school, is the site of the synthesis of the cell's product, secretory granules or yolk, for example. Jacobs believes that the internum increases at the expense of the externum, but Hirsch prefers to think of the externum as gathering and transporting materials from the cytoplasm to the internum. When the synthesis is complete, the product is rolled out of the system into the cytoplasm, and the "Golgi-remnant" remaining behind becomes new presubstance to repeat the cycle in polyphasic cells. The apparently missing osmiophobic component in vertebrate somatic cells, Hirsch thinks is to be found in the granule or vacuole that develops inside the net and that has been frequently overlooked by observers or ruled out of the Golgi picture as a case of Parat's "vacuome" and thus not a part of the apparatus. The network itself, except for a possible net of presubstance, Hirsch thinks is often an artefact of over-impregnation, since each internum has its own externum. Where many of these are aggregated within a small space they may overlap and appear continuous. There may be, however, in addition to the mono-systems, true poly-systems in which the externum may remain continuous around a group of internums. The recent studies by Worley and Worley (1943) and Worley (1943a, b, 1944a, b) seem to fit the Hirsch pattern almost exactly. The following diagram taken from Hirsch (1940a) summarizes these concepts.

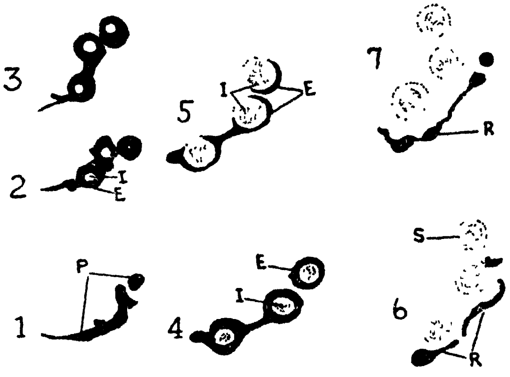

FIG. 3. HALF SCHEMATIC DIAGRAM OF THE SECRETION CYCLE OF THE GOLGI APPARATUS IN THE PANCREAS OR SALIVARY GLAND
E—externum; I—internum; P—presubstance; R—Golgi remnant; S—product (after Hirsch, 1940a)

In the same year that Hirsch's monograph appeared, a careful study of many amphibian tissues was made by Pollister (1939), in which the form of the Golgi apparatus was demonstrated, after careful measurements, often using all of the serial sections of a single cell, to consist of a plate-work of irregular shape but always of uniform thickness, about 0.2 of a micron. This study was purely morphological and based entirely on impregnated sections. Pollister's conclusions can best be illustrated by two schematized drawings from his paper, indicating his suggested classification of all cells into those that are polarized and those that are non-polarized, from the physiological angle. In this connection, Pollister classifies the cells of the adrenal medulla, embryologically related to nervous tissue, as the B or physiologically unpolarized type. Bennett (1941) has shown that in the cat these cells have a strict orientation, with one pole toward the venous capillary and the other toward an arterially supplied capillary. The secretion is toward the venous capillary, and nerves may be demonstrated in contact with the opposite end. The Golgi apparatus is polarized toward the vein.

As Pollister (1939) reminds us, the general arrangement of the Golgi apparatus among invertebrates seems to be that of a widely scattered distribution of discrete elements; that in the somatic cells of vertebrates is more often a compact polarized affair, whether it be made of separate units or fused into a net or plate-work or canal. Some recent studies do not fit this general pattern, as, for instance, Subramaniam (1939a), who found that in *Branchiostoma* the apparatus is unpolarized and not as usually found in the vertebrates; Sosa and Menegazzi (1940), who found networks in leech muscle; Dehorne (1938), who found it to be polarized in Nereis, and (1939b) unpolarized in the toad pancreas; James (1939), who reported in eosinophiles of the *Necturus* thymus a dispersed perinuclear Golgi apparatus, partly branching and partly in the form of isolated rings; and Filhol (1938), who found polarization in the pulmonates. Filhol developed an interesting theory that the pulmonates exhibit a kind of transitional stage between the two types of distribution since, though invertebrates, they usually have a Golgi zone but no network. In another paper Feyel and Verangot (1938) recall conclusions previously reached by the first author that excretory cells of invertebrates have a purely vacuolar Golgi apparatus (discrete elements), but that the higher we go in the animal series, the more complex it becomes.

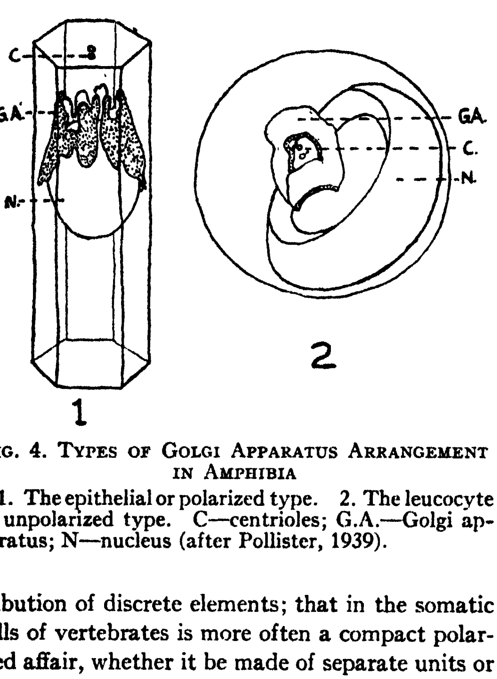

FIG. 4. TYPES OF GOLGI APPARATUS ARRANGEMENT IN AMPHIBIA

1. The epithelial or polarized type. 2. The leucocyte or unpolarized type. C—centrioles; G.A.—Golgi apparatus; N—nucleus (after Pollister, 1939).

The position of the Golgi apparatus has been studied for the most part in mononuclear cells, but the situation in multinuclear cells, where the nucleocytoplasmic interchanges or forces might be expected to differ from those in mononuclear cells, has been described by several recent observers. Rossman (1940) has found in deciduomata of monkeys the Golgi apparatus in multinuclear cells to be dispersed or to exhibit some anastomoses, but there is never any polarization with respect to the nuclei. In human lympho-ganglionic tissue in Hodgkin's disease, Buno (1938) found only one Golgi zone, no matter how many nuclei. It occupied the central space between the nuclei, if such a space existed. Watzka (1939) frequently found, in binucleate cells in rabbit sympathetic ganglia, a separate Golgi zone associated with each nucleus. Thus, at present, no common feature emerges as to the Golgi body's relation to the nuclei.

There have been several passing references to vacuoles and the vacuome hypothesis already in this paper, and no discussion of the form of the Golgi apparatus should fail to take account of the fact that vacuolar spaces or their walls frequently are blackened after osmic acid or silver nitrate impregnation. Kirkman and Severinghaus treat the matter as of historical interest only and claim that the whole idea that these structures might be Golgi apparatus has been completely disproved. Without evaluating the various researches which they marshall in support of this idea (p. 569), it may be said that other more recent publications, including those of Mahoney (1940), Clement (1938) and Champy and Coujard (1939), add a further weight of numbers to their list. There is, however, something to be said on the other side of the question. Cowdry (1938) has found no reason to depart from the idea of the relation of neutral red vacuoles to certain of the blackened nets in impregnated material, a relation such as he and Scott described in 1928, as occurring in the malarial parasite, where neutral red granules fuse to form an osmic impregnated Golgi net. Feyel and Verangot (1938) observed, in the normal human thyroid and in exophthalmic goitre, the vacuome (not to be confused with Bensley's vacuoles),—frankly so-called, although it was demonstrated by impregnation with silver nitrate and corresponded to what others have called the Golgi apparatus. They found that a concentration of the vacuome in a local region is characteristic of a stable metabolism, whereas a spreading of the vacuoles throughout the cytoplasm occurs during hyperactivity of the cell. In the latter case there is no Golgi zone. Filhol and Garrault (1938) found in the Golgi zone, in four species of selachians, only a vacuome-chondriome complex Feyel (1939) interpreted all silver nitrate blackened bodies in the guinea pig hypophysis as vacuoles with mitochondria on their surfaces Järvi (1939), working on the sublingual glands of the cat, figured a strikingly vacuolated Golgi apparatus, present especially in the protein cells and in the mucus cells, an hour after pilocarpine injection. Vetter (1940), by injecting trypan blue into mother mice and rats until their milk was blue, was able to observe blue vacuoles in the Golgi zone in the intestinal epithelium of the suckling babies. Hibbard (1942) saw neutral red vacuoles in the digestive tracts of chick embryos and young chicks, corresponding in every stage, even in cases of reversed polarity, to the position of the Golgi apparatus, although, since the impregnated apparatus was not visible in live cells, there was no proof as to whether the vacuoles were between the strands of the Golgi apparatus, or within them, or forerunners of them. Contrary to statements frequently appearing that Parat simply thought that the vacuoles were in reality the Golgi apparatus, because of their capacity for impregnation, that was but one aspect of his complete concept Stated in brief, he found that so many different things could be impregnated that it would be better to distinguish each of them by their individual names rather than lump them in one category. He differentiated: vacuoles, either separated or flowing together during fixation and impregnation; mitochondria, either ordinary chondriosomes or hypertrophied ones—he thought the dictyosomes of male germ cells and certain larger chondriosomes in special glands were of this type; diffuse cytoplasmic lipoids attracted to the interfaces of vacuoles or chondriosomes and the cytoplasm; or any combination of these. Recognizing the inter-relations between many of these cytoplasmic inclusions, Baker (1944) attempts to resolve the confusion by using the overall name "Golgi element" to include four parts: the vacuoles stainable by neutral red, the dense lipoid-containing substance (osmiophilic and stained by Sudan black), the Golgi product (secretion granule) and the diffuse lipoid-containing ground substance which fills in all the rest of the space in what others have called the Golgi zone. Parat noted, as many subsequent observers have done, that additional vacuoles were formed by the action of neutral red, and this fact has led some observers to conclude that all neutral red staining vacuoles are abnormal to the living cell, but there seems to be ample evidence that there is a normal vacuome existing in cells before the provocation of additional vacuoles by foreign agents. Worley (1943b) states, "It appears very probable that there is a correspondence between the 'vacuome' and the Golgi system in far more instances than we have been accustomed to believe." Related to the idea of a vacuolar form of the Golgi apparatus is the concept that it is a canal, such as that described by Simpson.

Thus the question as to the form of the Golgi apparatus is still far from a solution which receives unanimous support from all cytologists.

PHYSICAL CHARACTER

With regard to the physical nature of the Golgi apparatus, questions as to its specific gravity and its fluidity arise. Experiments with centrifugation throw light upon this subject. In earlier summaries the conclusion has been reached that the Golgi apparatus is lighter than the cytoplasm. It usually lies centripetal to the mitochondria, but Beams and King (1938), in 25 per cent of the guinea pig eggs centrufuged by them, found the yolk nucleus (Golgi apparatus) among the mitochondria at the heavy pole, and in the other 75 per cent it was nearer the middle but heavier than yolk, clear cytoplasm, and fat. Gresson (1940a), examining the mouse oocyte, found these bodies near the middle. Richter (1940) could not determine, in the spermatocytes of *Notonecta*, which was the centrifugal pole, but at some stages the idiosome spheres were not attached to their Golgi caps, and in such cases the two portions of the apparatus moved to opposite poles. The idiosome-Golgi cap complex, or the Golgi cap in the dissociated phase, moved to the same pole with the mitochondria. This seems to be another similarity of the male germ cell dictyosome with mitochondria (see p. 4).

As to the fluidity of the Golgi apparatus, it has been described both as very fluid and as relatively solid. New work adds evidence to both sides of the question. Pollister (1939) assumed that the Golgi apparatus cannot be fluid, nor even a highly plastic solid, and at the same time maintain its platelike form, though he found it elastic to the extent that bending due to pressure from the gastric contents is straightened again when the pressure is removed. At the opposite extreme are the views of Simpson (1941), who assumes it to be of the greatest fluidity because of its distortion upon freezing (see p. 11); and of Worley (1943b), who observed vesicular Golgi bodies readily collapsing and discharging their fluid contents into the cytoplasm when treated with hypertonic salt solutions.

CHEMICAL COMPOSITION

The widely accepted idea as to the chemical constitution of the Golgi apparatus is that it is lipoidal or lipo-proteic. MacLennan (1943) classified the intermediate lipoid bodies in the Protozoa among the Golgi bodies on the basis of the general acceptance of the lipoid constitution of the latter wherever found. Ever since the statement made by Sjövall in 1906 that the Golgi apparatus was lipoidal in nature, a statement not based on anything like modern histochemical tests, the literature has been full of tacit assumptions that it is lipoidal. Monné (1939b), using Helix spermatocytes observed under dark field illumination, found that by adding sodium bicarbonate solution, the dictyosomes (which he assumed to be the Golgi apparatus) became lighter in color, then swelled and showed a tendency to coalesce, and finally gave rise to typical myelin figures. His explanation for this behavior was that the lipoids in the shell of the Golgi apparatus gave rise to the myelin figures. (See fig. 5.) Baker (1944) proved by a variety of additional tests that these bodies in *Helix* probably contain lecithin or cephalin or both. The conspicuous dictyosomes that are found in spermatocytes clearly have lipoidal constituents, but that this is true of the more elusive apparatus of somatic cells is not so clear. There is a good deal of evidence that the germ cell dictyosomes are not the same thing as the blackened apparatus in many somatic cells (see p. 4), and if these are different categories of inclusions, the generalized statement that all Golgi bodies are lipoidal is unjustified.

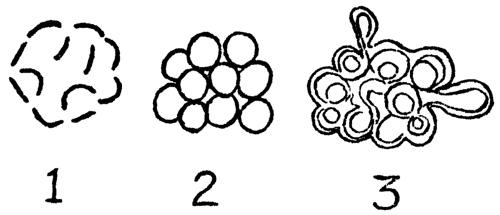

FIG. 5. THE EFFECT OF SODIUM BICARBONATE ON THE GOLGI BODIES IN HELIX SPERMATOCYTES

1. Golgi bodies in the normal state. 2. Golgi bodies assuming globular form in sodium bicarbonate. 3. Myelin figures growing out of Golgi bodies after a longer treatment with sodium bicarbonate (after Monné, 1939b).

MacLennan has stated that both lipoidal and non-lipoidal bodies in the Protozoa react identically to Golgi techniques. This author included among these, fatty acid bodies or intermediate lipoid bodies, granules and membranes associated with the contractile vacuole, and granules with a secretory cycle which are neither lipoidal nor excretory. However, he referred to the fatty acid bodies or intermediate lipoid bodies as Golgi bodies. Meglitsch (1940), on the other hand, considered the secretory granules to be the Golgi bodies, and found that they stain with neutral red. Still other workers identify the osmiophilic cortex of the contractile vacuole as the Golgi apparatus,—for example, Gatenby and Smyth (1940), who described its behavior in rapidly dividing and in non-dividing cultures of *Copromonas*. Smyth (1944) sums up the various Protozoan structures that have been described under the name of Golgi apparatus.

Much of the experimental work in centrifuging the apparatus to the lighter pole of the cell in Metazoa has been used to furnish proof of its lipoidal constitution. Bourne (1942), after stating that Golgi bodies are soluble in fat solvents and therefore contain a high percentage of fats, and mentioning their reduction of osmic acid and the centrifuging experiments, concludes that they are probably fatty and protein, with the latter on the outside, so that they cannot be stained with fat dyes. Watzka (1939) found that the Golgi apparatus breaks up and disintegrates after chloroform narcosis, suggesting that it has a lipoidal character. Hirsch thinks the presubstance blackens because of unsaturated fatty acids contained in it. He believes it must be a chemical mixture, possibly a different mixture in different cells, although it appears structureless; but this needs to be proved. Salazar (1943a) states that the Golgi apparatus may possibly be lipoidal or lipo-proteic but the the para-Golgi apparatus inside it is never lipoidal. Worley (1943a) assumes the Golgi body in molluscs to be a more or less spherical vesicle with a chromophilic, gel-like, relatively lipoidal pellicle covering a relatively more protein, fluid, chromophobic core.

Perhaps the most painstaking work on the chemistry of the apparatus is the work by Simpson (1941), and since Kirkman and Severinghaus expressed a hope that the method he used, the freezing-drying method, might throw much light on this aspect of the subject, a more extended review of Simpson's paper will be made. Since the cells (from epididymis, duodenum, and pancreas of the guinea pig, and spinal ganglion of the rabbit) were to be examined cytologically after the freezing-drying technique, careful controls were studied at each stage of the freezing and drying to determine where any artefacts due to freezing might be found. At slow speeds of freezing and even at certain zones parallel with the surface when freezing was very rapid, at −195°, there were damaged regions due to ice-crystal formation, but in the well-preserved areas, Simpson asserts that the fixation and preservation were superior in excellence to that in the best chemically fixed sections. The form of the apparatus proved in all cases to be a coiled canal, of uniform bore, within the cytoplasm. Examination of the frozen-dried Golgi apparatus by means of dark field illumination or with the polariscope showed no optical distinction from the surrounding cytoplasm. The contents of this canal could not be impregnated with osmic acid, nor even its surface, in pieces which were completely dried. In frozen bits of tissue which were allowed to thaw in Golgi fixatives and then impregnated, some blackening occurred, though it was not as clear as after the ordinary methods without freezing. It was usually the outside and not the contents of the canal which blackened. It appears that there is no lipoid or specific osmiophilic substance in the Golgi apparatus, unless it was altered by the freezing and drying. The apparatus was not readily stainable as thus prepared, but was clearly visible when the rest of the cell was stained. To test its possibly scanty lipoidal contents, tissues after freezing and drying were subjected to boiling absolute alcohol for 24 hours and subsequently to boiling anhydrous chloroform for another 24 hours, after which its stainability was found to be enhanced. Fine fibrils could be demonstrated inside the tubule, which stained with resorcin-fuchsin, from which fact Simpson concludes that the Golgi apparatus contains very diffuse proteins that were not stainable in the first instance because the protein molecules were too dispersed by faint traces of lipoidal material. When the vigorous fat extraction had been accomplished, the protein molecules were allowed to aggregate into the fine fibrils, which were stained as elastic fibers are stained by resorcin-fuchsin. (Weigl in 1910 was able to stain with this dye after bleaching an osmic impregnated nerve cell.) Injections of neutral red into animals before killing produced *de novo* droplets in the epididymis cells distal to the nucleus, in the area where the secretion granules were forming but distinct from the Golgi canal. While the Golgi apparatus after freezing and drying failed to show any impregnation with osmic acid, there were produced finely dispersed black granules throughout the cell. The point is not emphasized by Simpson but there is the possibility that a dispersed material or materials might accumulate during special chemical fixation in the fluid canal to give it the osmiophilic quality generally observed. Simpson indicates the high fluidity of the apparatus in the cells he studied, by pointing out that it is highly susceptible to "blowing up" on freezing in the imperfect zones of the block.

Vitamin A is apparently not associated with the Golgi apparatus. Since Popper (1944) has found it, in the liver and adrenal gland, practically always bound to intracellular lipids demonstrable by sensitive stains, its absence on or in the Golgi apparatus might be taken as additional evidence of the absence or very high degree of dispersion of lipoidal constituents in that apparatus.

Professor R. R. Bensley, who has done me the honor of reading this manuscript, is inclined to think of the Golgi apparatus, exclusive of that in spermatocytes, as a system of vacuoles or canals containing very highly dispersed lipoidal, protein, and other organic and inorganic constituents more or less specific for the type of cell containing it, and dependent, within limits, on the permeability of its surface membrane and the metabolism of the type of cell concerned. (Personal communication, 1944.) This suggested specificity of chemical composition to the type of cell is illustrated by Emmel (1945), who found alkaline phosphatase in abundance in the Golgi apparatus of the absorbing cells in the intestine but not in that of the absorbing cells of the proximal renal tubule.

FUNCTION

There is perhaps more agreement among cytologists that the Golgi apparatus is secretory in function than about any other aspect of the problem. And yet even here the questions as to whether it is transformed directly into the secretion product (as is the internum of the apparatus according to Hirsch, *et al.*), or whether the apparatus is instrumental in forming the secretion outside itself (Järvi, 1940), or whether it is only indirectly concerned, as shown by enlargement of the apparatus during the formation of the secretion products though it may not be in direct contact with the secretion (Aplington, 1942, Copeland, 1943, Deane, 1944a, b; Goormatigh. 1940). In the pancreas of the cat and mouse, Järvi (1939) found no great variation in the size of the Golgi net, but the secretion granules arise in its meshes. But there were reported no activities of the apparatus correlated with secretory cycles in most of the cells of the *Triturus* hypophysis (Copeland, 1943), in the hypophysis of the fowl (Payne, 1942), in the salivary glands of twenty species of Hemiptera (Baptist, 1941), in the adrenal of the cat (Bennett, 1940, 1941), or in neurosecretory cells in fish (Palay, 1943a). Reese and Moon (1938) reported some hypertrophy of the Golgi apparatus in the fascicular zone of the adrenal cortex after adrenocorticotropic hormone injection. Ponse (1938) found no hypertrophy, fragmentation, or disappearance of the Golgi apparatus in the thyroid, but she found some relation to the secretory pole of the cell, since in normal glands only one cell in 500 showed reversed polarity, while in glands activated by thyrotropic hormone one cell in 10 showed reversed polarity. Among the many publications adding evidence to the idea of the secretory activity of the Golgi apparatus are those by Hirsch and his associates (Järvi, Breitschneider, Jacobs, von Weel, Sluiter, Rinkel, *et al.*); in fact, their contribution is largely based on tracing the process of secretion formation by this structure in many types of cells. Also Subramaniam (1938b) found Golgi crescents adhering to watery and granular secretions, and from their shape and position assumed they secreted the enzymes in Lumbriconereis intestine cells. Aykroyd and Gatenby (1941) found in human uterine glands definite changes of the Golgi apparatus correlated with functional activity. Foster (1943) concluded that varying structure in cells of the parathyroid corresponds to functional cycles. Ayers (1941) observed vesicles moving out from the Golgi net in the young rat hypophysis and suggested the origin of the endocrine secretion by this means. Worley and Worley (1943) and Worley (1944a, b) described the synthesis of protein and fat both in and on the Golgi apparatus of mollusc embryos and larvae. Worley (1943a) finds its ability to absorb and to segregate materials from the cytoplasm to be its two most fundamental physiological characteristics Miller and Riddle (1942) thought that the Golgi net was not instrumental in the formation of lipoid granules in the pigeon adrenal cortex, but since the net expands later into fine strands between these granules it may play a part in transforming the precursor substance into the true hormone.

It is in connection with its secretory function that there is the greatest volume of evidence for the homology of the Golgi apparatus of germ cells with that of other cells, outside of its impregnation with osmic acid and silver nitrate. Worley (1939) compared the sperm-forming cells in decapods having nonflagellated spermatozoa with cells giving rise to the more usual flagellated spermatozoa, and assumed homologies in the completed cells based on similar transformations or secretions of duplex dictyosomes or Golgi bodies. So widespread is the idea that the Golgi apparatus is concerned with secretory phenomena that Dalton and Edwards (1942a, b) finding in hepatic tumors of rats and mice that the Golgi material remained invariable, as a condensed juxta-nuclear net, concluded from this that there was an absence of exocrine secretion. Dawson (1942) summarizes, "It is clear that no final disposition of the problem of the role of the Golgi apparatus in secretion can be made until cytologists decide whether the Golgi apparatus is a single entity of specific composition or a complex of several systems closely associated topographically, and perhaps functionally, within the cell."

There is some evidence, too, that the Golgi apparatus is concerned not only with secretion but with absorption (van Weel, 1938a, b, 1939; and Vetter, 1940). Pfuhl (1938) and Pfuhl and Dienstbach (1938) found that injected colloidal dyes and Chinese ink were absorbed by the liver cells into the Golgi apparatus.

An extraordinarily interesting aspect of the question has come to light in studies which localize vitamin C (ascorbic acid). Bourne (1942) thinks the vitamin goes inside the Golgi apparatus and there, protected from reactions in the general cytoplasm, it takes part in the synthesis of secretion products. Its position in the Golgi apparatus may also aid in the passage of substances across the placenta or the kidney tubule by protecting the diffusing substances from the powerful reducing action of the vitamin. Fischer (1938) observed changes in the polarity of the Golgi apparatus during diuresis.

Many substances have been reported to be adsorbed on the Golgi apparatus, including iron (Hirsch), lithium carmine and trypan blue (Fischer, 1938), various other metals (Van Tiel, 1940), benzpyrene (Graffi, 1940) and among them, vitamin C. Hirsch, however, suggests that the vitamin is not adsorbed by the apparatus but condensed by it. Among recent workers who showed the location of the vitamin to be in the Golgi apparatus may be cited Järvi (1940b), Faller (1941), and Tonutti (1940), who in addition figured its active emission from the apparatus in the functioning adrenal cell.

Barnett and Bourne (1941) found, in the early development of the chick, that during the first eighteen hours the vitamin was localized only in the peripheral cells of the blastoderm in contact with yolk granules. (Parat found the first "Golgi apparatus" in several invertebrate embryos in contact with yolk granules.) From the first to the third day it is in the extra-embryonic membranes only, but beginning with the fourth day, it is found in the cells of the embryo itself (central nervous system, liver, pancreas, myotome, etc.). They conclude that quantities of the vitamin in the reduced state are not necessary for the initial rapid growth; that while it is probably utilized by these early tissues (some blackening of blood vessel walls, coelomic cavity, and neural tube walls in the first three days may indicate its passage into the tissues), the oxidation potential in the young cells is so high that the vitamin is oxidized immediately on reaching the cells. It is well known that studies on the Golgi apparatus in these same earliest embryonic cells are rare, though many descriptions exist for later stages of embryology. Possibly the cellular differentiations at these early stages have not yet reached a point where a specialized protective region of the cytoplasm can conserve the reduced vitamin. However, Weed (1937) described a Golgi apparatus in the primitive muscle cells of a 40-hour chick embryo.

Barnett and Bourne (1941) also studied the later development of the chick embryo and concluded that the reduced silver deposits (vitamin C) in the liver, kidney, ovary, and nervous system were actually in the Golgi apparatus. They found no support for the view that the vitamin may be on or in the chondriosomes. They could find no deposits in cells of the testis. The account of Kehl (1939) presents the earliest picture of Golgi apparatus in the chick testis, and the primordial germ cells were there distinguished from the vegetative cells destined to form Sertoli cells by means of the orientation of the Golgi apparatus. This work, however, was done on chicks two to three days after hatching, while Barnett and Bourne studied embryos. Faller (1941) studied the vitamin C distribution in the testis of the rat but was apparently concerned only with the vegetative cells. It would be extremely interesting to know whether a difference in vitamin C content might be added to the numerous other differences between male germ cell dictyosomes and the Golgi apparatus of somatic cells.

Barnett (1942) found vitamin C in the Golgi material or on fat droplets in cultured heart, bone, and adrenal cells, but only in a few cells. Those with the greatest amount were degenerating cells. It will be remembered that Ludford stated that only in degenerating cells in tissue cultures could the Golgi apparatus be seen while the cells were alive and unstained. Barnett and Fisher (1943) further point out that, as in the deposition of osmic acid analysed by Bensley and Owen, the position of the precipitate on the Golgi substance does not prove that the vitamin was in that position in the functioning cell; the vitamin was somewhere in the cell, and the silver which is reduced by it may simply settle at an interface provided by two immiscible materials.

Since so much doubt has been cast on the reliability of impregnation methods for the demonstration of the Golgi apparatus, some consideration of the methods for the demonstration of the vitamin histologically are pertinent. While the Cajal and DaFano methods for Golgi apparatus depend on special fixation and subsequent reduction of the silver salt, the vitamin C reaction depends on direct reduction (see Giroud, 1938; Barnett and Bourne, 1941). The resulting blackening parallels the results obtained by the chemical method of titration with dichlorophenolindophenol and also the biological findings on the antiscorbutic action of the vitamin. In those animals which are unable to synthesize Vitamin C, and which are subjected to a scorbutic diet, the cellular granules progressively disappear. Reduced silver granules are not produced by other cellular reducing agents; removal of lipoids from the cell by chloroform does not change the reaction, though aqueous solutions may wash out the vitamin.

TECHNIQUES OF INVESTIGATION

Recognizing the sorry state of affairs existing because of conflicting interpretations based upon the only diagnostic methods of demonstrating the Golgi apparatus, by means of impregnations, many investigators have attempted to find out what we are dealing with by other means, always returning to impregnations to be sure they were correctly identifying it. Thus, as has already been mentioned, displacing the Golgi apparatus by means of centrifuging and the freezing-drying technique have been tried. Parat's followers still use "techniques convergantes," by which they mean that all types of fixatives and stains, including histochemical tests and vital examination are focussed on a given cell. The "Stufenuntersuchungsmethode" is used by Sluiter and others in Hirsch's school, meaning a study of the cell through all its functional phases.

The physiological state of cells has been experimentally altered by feeding (van Weel, 1938a, 1939); or by hormone action (Ponse, 1938; Reese and Moon, 1938; Miller and Riddle, 1942; *et al.*); or by starvation (De Robertis, 1939); or by temperature variations (Radsma and van Weel, 1940, who raised rats from a tropical environment in cool surroundings and found their thyroid Golgi apparatus disappeared in thirty days, not to reappear as a normal reticulum until the third generation); or by varying the water balance (Fischer, 1938; Emmel, 1938); or by forcing a muscle cell to work. Roskin (1938) found no change in the Golgi apparatus of the smooth muscle of Amphibia after five hours of working in vitro; but Sosa and Menegazzi (1940) were able to demonstrate changes in structure with contractile activity in the leech muscle. Waugh (1942) found that various sulphonamides affect the Golgi apparatus in the chick embryo, causing fragmentation. Dooley (1941) found the dictyosomes of male germ cells of Orthoptera to be peculiarly resistant to changes resulting from high concentrations of colchicine which altered all other cytoplasmic inclusions.

Different methods of observation have been used by Monné (1939a), who used the dark field illumination on *Helix* spermatocytes already described. Viewing them by means of polarized light, Monné (1939b) also found that the outer part of the Golgi bodies in these pulmonate spermatocytes is birefringent, though he cautions that the light must be of the strongest possible intensity, and that though visible unstained, they are much more brilliant when vitally stained with chrysoidin. The Golgi elements are lens-shaped with an outer layer which he concluded contains lipoid molecules perpendicular to the surface. It will be recalled that Simpson found no optical differences by using Monné's methods of illumination.

Tarao (1940) found that after over-night digestion in trypsin of formol fixed sections of mouse pancreas, it was possible to stain the Golgi apparatus with Nile blue sulphate. Worley and Worley (1943) used vital staining with methylene blue to demonstrate it.

CONCLUSION

So we are back at the point where we started. In the face of the statements by Kirkman and Severinghaus (p. 558) that "The literature records instance after instance in which intracellular vacuoles or canals, preformed or induced, prozymogen granules, intracellular lipoids, deposits of osmium on Nissl bodies and mitochondria have been mistaken for Golgi material" (bibliographical references omitted), and farther on, that "it seems likely that mistaking the identity of the Golgi apparatus in most vertebrate cells at least, is largely a thing of the past," examination of current literature nevertheless reveals vesicles or vacuoles (Worley), intracellular canal (Simpson), prozymogen granules (Hirsch), intracellular lipoids (MacLennan, and Guthrie and Jeffers), and modified mitochondria (Filhol, Feyel, and Dehorne), all identified as Golgi apparatus. Progress cannot be made by confusing unlike structures.

In conclusion, the Golgi apparatus might still be defined as that cytoplasmic structure or structures which blacken with osmic acid or silver nitrate and which, in the opinion of the observer, is not something else. The lack of unanimity on every aspect of the subject strongly suggests that cytologists are not all studying the same thing, in spite of the fact that they all use the same name for it. This review of recent findings proves that more than one category of inclusion is still being blackened and described under the name "Golgi apparatus," and that efforts to generalize by assuming that the behavior, structure, and physicochemical composition observed in any one case are applicable to the "Golgi apparatus" in the abstract sense cannot but result in contradictions. With regard to most of the generalizations, we should be better off if the discovery of the impregnation methods had never been made.

There are, however, some bright spots. To quote Okkels (1934), "It is true that the classical Golgi apparatus is more or less an artefact. But it is a regular one, claiming as such scientific importance." Artefact or not [Tarao (1940): "The Golgi apparatus . . . is too beautiful to be an artefact"], when it varies regularly with functional states in a given cell, it indicates something, even though we do not know what, about the activity of that cell. Its diagnostic value has been mentioned. And the dictyosomes of male germ cells are certainly not artefacts. Though it seems unlikely that they are the same as other structures bearing the name Golgi apparatus, observations of their peculiar behavior during spermiogenesis have added to our knowledge of that process.

The decrease in the number of papers dealing with what is still a much misunderstood, as well as little understood, field of research appears to be due less to any general agreement among cytologists as to a solution of the problem involved, than to a disillusionment with regard to the methods employed to find those solutions. Since the methods of metallic impregnation bring forth only morphological features, and since even these methods are not specific, some other avenue of approach becomes necessary. Thus, Guthrie and Jeffers (1938), assuming that, in egg cells at least, "so-called Golgi bodies" are products of cellular metabolism, state: "We do not use this designation" (Golgi apparatus) "because of the vitalistic concepts that have become associated with it." D'Arcy Thompson (1942) points out "the inevitable fact that dynamical problems lie behind the morphological problems of the cell." This idea is surely in the minds of cytologists who go to so much trouble to describe the morphological aspects, as evidenced by Parat's reasoning that the vacuome-chondriome complex as he saw it in spermatocytes and in gland cells was important as a means of separating yet keeping close together, different solvents in order to orient molecules for syntheses. Hirsch goes to some trouble to suggest the similarity of coacervates and the surfaces of the Golgi apparatus. But these and similar suggestions arise more from thinking about the apparatus than from direct observation of it. It may well be that until we can attack the whole problem of cellular functioning in a more minute manner, further discussions about the materials blackened by metallic impregnations are fruitless. Needham (1942) reminds us that "the chemical structure of molecules, the colloidal conditions in the cell and the morphological patterns so arising, are inextricably connected. . . . We are driven to the view that the living cell possesses as complex a set of interfaces, oriented catalysts, molecular chains, reaction vessels etc., as the organs, tissues and other anatomical structures of the whole organism." In these terms our present knowledge is in the most elementary, gross form.

LIST OF LITERATURE

(With few exceptions the literature citations are from 1938 on.)

ANDREW, WARREN. 1939. The Golgi apparatus in the nerve cells of the mouse from youth to senility. *Amer. J. Anat.*, 64: 351–375.

ANGELO, SAVINO D'. 1941. An analysis of the morphology of the pituitary and thyroid glands in amphibian metamorphosis. *Amer. J. Anat.*, 69: 407–437.

——, and HARRY A. CHARIPPER. 1939. The morphology of the thyroid gland in the metamorphosing *Rana pipiens*. *J. Morph.*, 64: 355–372.

APLINGTON, HENRY W., JR. 1942. Correlative cyclic changes in the hypophysis and gonads of *Necturus maculosus* Rafinesque. I. The male. *Amer. J. Anat.*, 70: 201–249.

AYERS, JOHN C. 1941. The Golgi material in the hypophyseal cells of the immature albino rat. *Anat. Rec.*, 81: 433–441.

AYKROYD, OLIVE E. 1938. The cytoplasmic inclusions in the oogenesis of man. *Z. Zellforsch.* 27: 691–710.

——, and J. BRONTË GATENBY. 1941. Cytology of human uterine glands in gravid and non-gravid phases. *Quart. J. Micr. Sci.*, 82: 541–562.

BACHMAN, RUDOLF. 1939. Über die Nebennierenrinde des Meerschweinchens während der Tragzeit. *Z. mikr.-anat. Forsch.*, 45: 157–178.

BAILLIF, RALPH N. 1941. Reaction of the rat omentum to injections of particulate matter. *Proc. Soc. Exp. Biol. Med.*, 47: 409–414.

BAKER, JOHN R. 1942. Some aspects of cytological technique. Chap. 1, *Cytology and Cell Physiology* (Ed., G. Bourne). Oxford: Clarendon Press.

——. 1944. The structure and chemical composition of the Golgi element. *Quart. J. Micr. Sci.*, 85: 1–71.

BAPTIST, B. A. 1941. The morphology and physiology of the salivary glands of Hemiptera-Homoptera. *Quart. J. Micr. Sci.*, 83: 91–139.

BARNETT, S. A. 1942. Observations on the distribution of ascorbic acid (vitamin C) in explanted cells. *J. Exp. Biol.*, 19: 88–91.

——, and G. BOURNE. 1941. The distribution of ascorbic acid (vitamin C) in the early stages of the developing chick embryo. *J. Anat.*, 75: 251–264.

——, and R. B. FISHER. 1943. Experiments on the silver nitrate method for the histological demonstration of ascorbic acid (vitamin C). *J. Exp. Biol.*, 20: 14–15.

BHATTACHARYA, D. B., and MURLI DHAR LAL SRIVASTAVA. 1939. The yolk nucleus of Balbiani. *Allahabad Univ. Studies, Zool. Sect.*, 1–11.

BEAMS, H. W. 1943. Ultracentrifugal studies on cytoplasmic components and inclusions. In *Frontiers in Cytochemistry* (Ed., Normand L. Hoerr), 71–90. Lancaster, Pa.: Jaques Cattell Press.

——, and R. L. KING. 1938. A study of the cytoplasmic components and inclusions of the developing guinea pig egg. *Cytologia*, 8: 353–367.

——, and J. F. SHEEHAN. 1941. The yolk nucleus complex of the human ovum. *Anat. Rec.*, 81: 545–557.

BENNETT, H. STANLEY. 1940. The life history and secretion of the cells of the adrenal cortex of the cat. *Amer. J. Anat.*, 67: 151–227.

——. 1941. Cytological manifestations of secretion in the adrenal medulla of the cat. *Amer. J. Anat.*, 69: 333–381.

BOURNE, GEOFFREY. 1942. Mitochondria and the Golgi apparatus. Chap. 4, *Cytology and Cell Physiology*. Oxford: Clarendon Press.

BUNO, WASHINGTON. 1938. L'appareil de Golgi de la cellule de Sternberg. *Bull. d'Histol. Appl.*, 15: 5–9.

CARTER, G. S. 1928. On the structure of the cells bearing the velar cilia of the nudibranch veliger. *J. Exp. Biol.*, 6: 97–109.

CHAMPY, C. H., AND R. COUJARD. 1939. Observations cytologiques et biologiques sur la spermatogénèse de quelques Batraciens et les caractères sexuels secondaires. *Arch. Zool. Exp.*, 81: 78–100.

CHATTON, E., and O. TUZET. 1941. Sur quelques faits nouveaux de la spermiogénèse du *Lumbricus terrestris*. *C. R. Acad. Sci. Paris*, 213: 323–376.

CLEMENT, R. 1938. On the cytoplasmic inclusions in the oogenesis of *Lepus cunniculus*. *Allahabad Univ. Studies*, 14: 137–174.

COPELAND, D. EUGENE. 1943. Cytology of the pituitary gland in developing and adult Triturus viridescens. *J. Morph.*, 72: 379–401.

COWDRY, E. V. 1938. *Textbook of Histology*. Philadelphia: Lea and Febiger.

DALTON, A. J., and J. E. EDWARDS. 1942a. Mitochondria and Golgi apparatus of induced and spontaneous hepatomas in the mouse. *J. Nat. Cancer Inst.*, 2: 565–575.

——, and ——. 1942b. Cytology of hepatic tumors and proliferating bile duct epithelium in the rat induced with p-dimethylaminoazobenzene. *J. Nat. Cancer Inst.*, 3: 319–329.

DAS, RAM SARAN. 1939. The cytoplasmic inclusions in the oogenesis of *Rhipcephalus sanguineus* (Latrielle). *Z. Zellforsch.*, 30: 36–51.

DAWSON, A. B. 1942. Some morphological aspects of the secretion process. *Federation Proc.*, 1: 233–240.

DEANE, HELEN W. 1944a. A cytological study of the diurnal cycle of the liver of the mouse in relation to storage and secretion. *Anat. Rec.*, 88: 39–65.

——. 1944b. A cytological study of storage and secretion in the developing liver of the mouse. *Anat. Rec.*, 88: 161–173.

DEHORNE, A. 1938. Formes sécrétantes du chondriome modifié. *C. R. Soc. Biol. Paris*, 128: 964–967.

——. 1939. Un exemple de modification du chondriome dans le sens d'un apport figuré à la prosécrétion. *C. R. Soc. Biol. Paris*, 130: 892–894.

DOOLEY, THOMAS P. 1941. The influence of colchicine upon the germ cells of insects (Orthoptera) with special reference to the mitochondria and dictyosomes. *Trans. Amer. Micr. Soc.*, 60: 105–119.

DORNESCO, TH. G. 1938. Sur la nature de l'appareil de Golgi des neurones des ganglions rachidiens des vertébrés. *C. R. Soc. Biol. Paris*, 129: 1232–1234.

DUMITRESCO, MARGUERITE. 1938. Les glandes séricigènes tubulaires de *Theridium tepidariorum*. *Arch. Zool. Exp.*, 79: 55–68.

EDWARDS, J. E., A. J. DALTON, and H. B. ANDERVONT 1942. Pathology of a transplantable spontaneous hepatoma in a C 3 H mouse. *J. Nat. Cancer Inst.*, 2: 555–563.

EMMEL, U. M. 1938. The Golgi apparatus in the proximal and distal tubule cells of the perfused frog's kidney. *Anat. Rec.*, 70: 371–384.

——. 1945. Alkaline phosphatase in the Golgi zone of absorbing cells of the small intestine. *Anat. Rec.*, 91: 39–47.

FALLER, ADOLPH. 1941. Histochemische Untersuchungen über das Vorkommen von Ascorbinsäure im Hoden und Nebenhoden von Ratten verschiedener Lebensalter. *Z. mikr.-anat. Forsch.*, 49: 333–358.

FEYEL, PIERRE, and JACQUES VARANGOT. 1938. Recherches cytologiques sur la glande thyroïde normale et pathologique (maladie de Basedow). *Ann. Anat. Path.*, 15: 136–164.

FEYEL, THERÈSE. 1939. Sur les constituants cytoplasmiques et sur l'évolution de la cellule acidophile dans la pars anterior de l'hypophyse du cobaye. *C. R. Soc. Biol. Paris*, 131: 560–562.

FILHOL, J. 1938. Recherches sur la nature des lépidosomes et les phénomènes cytologiques de la sécrétion chez les Gasteropods pulmonés. *Arch. Anat. Micr.*, 34· 155–218; 375–439.

——, and G. GARRAULT. 1938. La sécrétion de la prokératine et la formation de la capsule ovulaire chez les sélaciens. *Arch. Anat. Micr.*, 34: 105–145.

FISCHER, HERMANN. 1938. Das Verhalten des Golgi-Apparates in den Hauptstückzellen der Harnkanälchen bei experimentell gesteigerter und gehemmter Diurese. *Z. mikr.-anat. Forsch.*, 43: 342–361.

Foster, C. L. 1943. Studies on the parathyroid of the mouse. *J. Endocrinol.*, 3: 244–253.

Gatenby, J. B. 1943. A nuclear ring in the developing male germ cells of the dog and cat. *Nature, London*, 152: 79.

——, and L. Collery. 1943. Middle piece beads in the Cavia spermatozoon. *Nature, London*, 151: 253–254.

——, and J. D. Smyth. 1940. The Golgi apparatus and pyrenoids of *Chilomonas paramecium*, with remarks on the identification of *Copromonas subtilis*. *Quart. J. Micr. Sci.*, 81· 595–617.

Giroud, A. 1938. L'acide ascorbique dans la cellule et les tissus. *Protoplasma Monog.*, 16: 1–187.

Goormaghtigh, N. 1940 Le cycle glandulaire de la cellule endocrine de l'artériole rénale du lapin. *Arch. Biol. Paris*, 51· 293–311.

Graffi, A. 1940. Intracelluläre Benzpyrenspeicherung in lebenden Normal- und Tuzmorellen. *Z. Krebsforsch.*, 50: 196–219.

Gresson, R. A. R. 1940a. A cytological study of the centrifuged oocyte of the mouse. *Quart. J. Micr. Sci.*, 81: 569–583.

——. 1940b. Presence of the sperm middle piece in the fertilized egg of the mouse (*Mus musculus*). *Nature, London*, 145: 425.

Guthrie, Mary J., and Katharine R. Jeffers 1938. A cytological study of the ovaries of the bats *Myotis lucifugus* and *Myotis grisescens*. *J. Morph.*, 62· 523–557.

Hibbard, Hope. 1942. The Golgi apparatus during development in the stomach of *Gallus domesticus*. *J. Morph.*, 70: 121–150.

Hirsch, G. C. 1938. Uber die Praesubstanz der Golgi-System. *Proc. Kon. Ned. Akad. Wet.*, 41: 840–846.

——. 1939a. Form- und Stuffwechsel der Golgi Korper. *Protoplasma Monogr.*, 18· 1–394.

——. 1939b. Einiges uber die Restitution von Produkten in tierischen Zellen. *Vhl. dtsch zool. Ges*, 41: 255–295.

——. 1940a. Vitamin C und Golgi-Korper. *Protoplasma*, 34: 377–392.

——. 1940b. Over het aandeel van het vitamine C in de opbouw van producten in cellen. *Natuurwetenschap. Tijdschr.*, 21: 363–370. (seen only in *Biol. Abstr.*, 16: no. 690.)

——. 1940c. Der intraplasmatische Stoffwechsel in den Darmzellen von *Ascaris lumbricoides*. *Protoplasma*, 35: 280–288.

Ito, T. 1941. Über den Golgiapparat und die Mitochondrien der Spermatogonien sowie Spermatozyten des Menschen, nebst Bemerkungen der Riesenspermatogonien. *Cytologia*, 11: 436–451.

James, Emory S. 1939. The morphology of the thymus and its changes with age in the neotonous Amphibian (*Necturus maculosus*). *J. Morph.*, 64: 455–482.

Järvi, Osmo. 1939. Über die Restitution des Sekretstoffes in der grossen Unterzungendrüse der Katze, geprüft durch die Stufenuntersuchungsmethode. *Z. Zellforsch.*, 30: 98–155.

——. 1940a. Über die sogenannten "Lipochondrien" von Ries in der Pankreaszelle und ihre Beziehung zu den Pigmenten. *Z. Zellforsch.*, 31: 1–42.

——. 1940b. Die Beziehungen zwischen dem Vitamin C und der Golgi-Substanz im exokrinen Gewebe des Pankreas und in den Speicheldrüsen der Katze. *Protoplasma*, 34. 362–376.

——. 1940c. Entgegnung auf die Bemerkungen von G. C. Hirsch über meine Arbeit: Die Beziehungen zwischen dem Vitamin C und der Golgi-substanz. *Protoplasma*, 35: 274–279.

Kehl, R. 1939. Sur la polarité de l'appareil de Golgi dans les elements des tubes sexuels mâles chez les Oiseaux. *C. R. Soc. Biol. Paris*, 131 104–106.

Kirkman, Hadley, and A. E. Severinghaus. 1938 A review of the Golgi apparatus. *Anat. Rec.*, 70: 413–431, 557–573; 71: 79–103.

Krichesky, B., and H. Mandel. 1943. The Golgi apparatus in uterine gland cells during pregnancy in the rabbit. *Univ. Cal. Pub. Zool.*, 47: 169–174.

Ludford, R. J. 1935. The cytological action of methylene blue. *Arch. exp. Zellforsch.*, 17: 339–359.

—— 1942. Pathological aspects of cytology. Chap. 8, Cytology and Cell Physiology (Ed., G. Bourne) *Oxford:* Clarendon Press.

MacLennan, R. F. 1939. Cytoplasmic inclusions. Chap. 3, Protozoa in Biological Research (Eds., G. N. Calkins and F. M. Summers). *New York:* Columbia Univ. Press.

—— 1940. A quantitative study of osmic acid impregnation in Protozoa *Trans. Amer. Micr. Soc.*, 59· 149–159.

——. 1943. Centrifugal stratification of granules in the ciliate *Ichthyophthirius* *J. Morph.*, 72: 1–25.

Mahoney, Florence Jerome. 1940. Spermatogenesis with special reference to certain extranuclear structures in the Pulmonate *Physa gyrina* Say. *Univ. Colo. stud. Gen. Sci.*, 26: 81–83.

McCroan, J. E., Jr. 1940. Spermatogenesis of the crayfish, *Cambarus virilis*, with special reference to the Golgi material and mitochondria. *Cytologia*, 11: 136–151.

McManus, J. F. A. 1943 Apparent reversal of position of the Golgi element in the renal tubule. *Nature, London*, 152: 417

Meglitsch, Paul 1940. Cytological observations on *Endamoeba blattae*. *Univ. Ill. Biol. Mongr.*, 17: 1–140.

Miller, Richard A., and Oscar Riddle. 1942. The cytology of the adrenal cortex of normal pigeons and in experimentally induced atrophy and hypertrophy. *Amer. J. Anat.*, 71: 311–341.

Monné, Ludwik. 1939a. Polarizationsoptische Untersuchungen über den Golgi-Apparat und die Mitochondrien männlicher Geschlechtszellen einiger Pulmonaten-Arten. *Protoplasma,* 32: 184–192.

——. 1939b. Über die Farbenveränderung der Mitochondrien und des Golgi-Apparates im Dunkelfeld. *Arch. exp. Zellforsch.,* 23: 157–168.

Needham, Joseph. 1942. *Biochemistry and Morphogenesis.* Cambridge: Cambridge Univ. Press.

Okkels, Harald. 1934. Dynamic cytology of the thyroid gland. *Arch. exp. Zellforsch.,* 15: 343–347.

Palay, Sanford L. 1943a. The origin of neurosecretory granules from the nuclei of nerve cells in fishes. *Anat. Rec.,* 85: 331.

——. 1943b. Neurosecretion. V. The origin of neurosecretory granules from the nuclei of nerve cells in fishes. *J. Comp. Neur.,* 79: 247–274.

Parat, Maurice. 1928. Contribution à l'étude morphologique et physiologique du cytoplasme. *Arch. Anat. Micr.,* 24: 73–356.

Payne, Fernandus. 1942. The cytology of the anterior pituitary of the fowl. *Biol. Bull.,* 82: 79–111.

Peyron, Albert, and Guy Pumeau Delille. 1938. Sur la signification des cellules claires et des inclusions observées dans le papillo-épithéliome de Shope. *C. R. Soc. Biol. Paris,* 129: 1114–1116.

Pfuhl, Wilhelm. 1938. Über die funktionellen Beziehungen zwischen den Leberzellen und den Kupfferzchen Sternzellen. *Anat. Anz.,* 86: 273–295

——, and Oskar Dienstbach. 1938. Die Speicherung und Verarbeitung von kolloiden Farbstoffen, Pigmenten und Lipoiden in der Golgi-Substanz der Leberzellen. *Z. Anat. Entwgsch.,* 108: 260–282.

Pollister, Arthur Wagg. 1939. The structure of the Golgi apparatus in the tissues of Amphibia *Quart. J. Micr. Sci.,* 81: 235–271.

Ponse, Kitty. 1938. Histophysiologie de l'activation thyroïdienne. *Rev. Suisse Zool.,* 45: 441–449.

Popper, Hans. 1944. Distribution of vitamin A in tissue as visualized by fluorescent microscopy. *Physiol. Rev.,* 24: 205–224.

Poris, Ethel G. 1941. Studies on the endocrines of reptiles. II. Variations in the histology of the hypophysis of *Anolis carolinensis* with a note on the Golgi configuration in cells of the pars anterior and pars intermedia. *Anat. Rec.,* 80: 99–121.

Radsma, W., and P. B. Van Weel. 1940. De Golgi-substantie in het schild-klierepithelium bij witte ratten in tropische en in koele omgeving Geneesk. *Tijdschr. Nederland.-Indie,* 88: 2858–2864. (Seen only in *Biol. Abstr.,* 15: no. 11755).

Rathnavathy, C. K. 1941. The spermatogenesis of *Clibanarius olivaceous* Henderson. *Proc. Ind. Acad. Sci. B.,* 13: 379–421.

Rauramo, M., and E. Turpeinen. 1940. Über die feineren Zellstrukturen bei Carcinoma corporis uteri. *Acta Soc. Med. Fennica Duodecim. B,* 29: 164–199. (Seen only in *Biol. Abstr.,* 17: no. 5033.)

Reese, J. D., and H. D. Moon. 1938. The Golgi apparatus of the cells of the adrenal cortex after hypophysectomy and on the administration of the adrenocorticotropic hormone. *Anat. Rec.,* 71: 543–556.

Richter, Kenneth M. 1940. A study of the cytoplasmic structures in the male germinal cells of several species of *Notonecta,* with special reference to the Golgi system. *J. Morph.,* 67: 489–522.

——. 1942. An experimental study of the cytology of human peripheral blood neutrophiles and lymphocytes. *J. Morph.,* 71: 53–76.

Rinkel, G. L., and G. C. Hirsch. 1940. Die Restitution des Eiweiss-secretes zum Nestbau beim Stickling *Gasterosteus* in Verbindung mit dem Arbeitsrhythmus der Niere. *Z. Zellforsch.,* 30: 649–688.

Robertis, E. De. 1939. Action du jeûne prolongé sur la cytologie hépatique de *Bufo arenarum* (Hinsel). *C. R. Soc. Biol. Paris,* 130: 299–300.

——. 1941. The intracellular colloid of the normal and activated thyroid gland of the rat studied by the freezing-drying method. *Amer. J. Anat.,* 68: 317–337.

Roskin, G. R. 1938. Contribution à la cytophysiologie de la cellule musculaire lisse de l'Axolotl. *Bull. Histol. Appl.,* 15: 57–66.

Rossman, Isadore. 1940. The deciduomal reaction in the Rhesus monkey (*Macaca mulatta*). *Amer. J. Anat.,* 66: 277–342.

Salazar, A. L. 1936. Sur le système para-Golgien or système tannophile de la zone de Golgi, révélé par la méthode tanno-ferrique. *Arch. Anat., Histol., Embryol.,* 21: 65–95.

——. 1942 L'appareil para-Golgi et les conceptions actuelles sur la zone de Golgi. *Anat. Rec.,* 82: 309–326.

Sato, I. 1940. Studies on the cytoplasmic phenomena in the spermatogenesis of the oriental scorpion, *Buthus martensii,* with special reference to the structure of the chondriome ring and the dictyokinesis. *J. Sci. Hirosoma Univ. B,* 8: 1–116. (Seen only in *Biol. Abstr.,* 15: no. 14153.)

Seshachar, B. R. 1942. Origin of interlocular oocytes in male Apoda. *Proc. Ind. Acad. Sci. B,* 15: 278–279.

Simpson, William L. 1941. The application of the Altmann method to the study of the Golgi apparatus. *Anat. Rec.,* 80: 329–343.

Singh, B. N., and W. Boyle. 1938. The vitellogenesis of *Gasterosteus aculeatus* (the stickleback) investigated by the ultracentrifuge. *Quart. J. Micr. Sci.,* 81: 81–108.

Sluiter, J. W. 1940. Die Cytologie, wahrend der ersten Phasen der Ovogenese, das Huhnereies. *Protoplasma,* 34: 393–430.

SMYTH, J. D. 1943. The Golgi apparatus in *Astasia harrisii*. *Nature, London*, 151: 110.

——. 1944. The Golgi apparatus of Protozoa. *Biol. Rev.*, 19: 39–47.

SOSA, J. M., and J. A. MENEGAZZI. 1940. The Golgi apparatus of striated muscle fibers of *Hirudo medicinalis* and its relation with contractile activity. *Arch. Soc. Biol. Montevideo*, 10: 6–14.

STEIN, K. F., ELIZABETH CALDWELL, and JEAN PETERS. 1942. Age changes in the anterior pituitary gland of the mouse. *Anat. Rec.*, 84: 523.

SUBRAMANIAM, M. K. 1938a. Studies on the structure of the Golgi apparatus. II. Liver cells of *Rhacophorus maculatus* Gray. *Proc. Ind. Acad. Sci.*, 7: 80–103.

——. 1938b. Studies on the structure of the Golgi apparatus. III. Some observations on the mechanism of secretion of the Golgi bodies in the intestinal cells of Lumbriconereis. *Proc. Ind. Acad. Sci.*, 7: 125–131.

——. 1939a. Studies on the structure of the Golgi apparatus. IV. Endostyle of *Branchiostoma indicum*. *Quart. J. Micr. Sci.*, 81: 429–450.

——. 1939b. Studies on the structure of the Golgi apparatus. V. The idiosome in the pancreas of the toad and its possible relation to ergastoplasm. *Proc. Ind. Acad. Sci*, 9: 271–286.

TARAO, S. 1939. Microchemical studies on the Golgi apparatus using protease-Nile blue sulphate techniques. I. The Golgi apparatus in hepatic cells in the mouse and newt. *J. Fac. Sci. Hokkaido Imp. Univ. Ser. VI*, 7. 1–16.

——. 1940. Microchemical studies on the Golgi apparatus using protease-Nile blue sulphate techniques. II. Golgi apparatus of pancreatic acinar cells of the mouse in fixed and living condition. *Cytologia*, 11: 261–281.

THOMPSON, D'ARCY. 1942. *On Growth and Form.* Second Ed. Cambridge: Cambridge Univ. Press.

TONUTTI, E. 1939. Über den Golgi-Apparat. *Vhl. Anat. Ges.*, 88: 78–81.

——. 1940. Die Vitamin-C-Darstellung im Gewebe und ihre Bedeutung zur funktionellen Analyse von Histosystemen. *Z. mikr.-anat. Forsch.*, 48: 1–53.

TURNER, JOHN B. 1940. Cytoplasmic inclusions in the ciliate *Tillina canalifera*. *Arch. Protistenk.*, 93: 255–272.

TUZET, O. 1938. Sur las spermatogénèse du *Buthus occitanus* (Amor). *Arch. Zool. Exp.*, 80: 335–351.

VAN TIEL, N. 1940. Der intraplasmatische Stoffwechsel in den Darmzellen von *Ascaris lumbricoides*. IV. Die Adsorption von Metallen an Golgi Korpern. *Protoplasma*, 35: 289–297.

VETTER, JOACHIM. 1940. Über die Frage der Beteiligung der Basalkörnten Zellen an den Resorptions- und Sekretionsvorgängen des Darmes. *Z. mikr.-anat. Forsch.*, 47: 33–48.

WALLRAFF, JOSEF. 1939a. Beiträge zur Morphologie und Morphogenese der Hypophysenzellen des erwachsenen Menschen. *Z. mikr.-anat. Forsch.*, 45: 631–667.

——. 1939b. Neue Untersuchungen an der menschlichen Hypophyse. *Vhl. Anat. Ges.*, 88: 94–95.

WATZKA, MAX. 1939. Vanänderungen des Golgi-Netzapparates nach Chloroformnarkose. *Z. mikr.-anat. Forsch.*, 46: 622–626.

WAUGH, J. G. 1942. Damage to the liver following sulphonamides. *Irish J. med. Sci., Ser.* 6: 607–610.

WEATHERBY, J. H. 1941. The contractile vacuole. Chap. 7, *Protozoa in Biological Research* (Eds., G. N. Calkins and F. M. Summers) New York: Columbia Univ. Press.

WEED, ISABELLE G. 1937. Cytological studies of developing muscle with special reference to myofibrils, mitochondria, Golgi apparatus and nuclei. *Z. Zellforsch.*, 25: 516–540.

WEEL, P. B. VAN. 1938a. Beiträge zur Histophysiologie des Dünndarmes. I. Zur Histophysiologie des absteigenden Dünndarmschenkels vom Reiher (*Ardea cimerea* L.). *Z. Zellforsch.*, 28: 62–82.

——. 1938b. Beiträge zur Histophysiologie des Dünndarmes. II. Zur Histophysiologie des Dünndarmes vom Frosch. *Z. vergl. Physiol.*, 26: 35–66.

——. 1939. Beiträge zur Histophysiologie des Dünndarmes. III. Die Veränderungen in den Darmdrüsenzellen während der Verdauung und in den Resorptionszellen wahrend der Fettresorption. *Z. Zellforsch.*, 29: 750–777.

WELCH, G. STUART, and ALBERT C. BRODUS. 1940. Golgi apparatus of the thyroid gland. *Arch. Path.*, 29: 759–772.

WILSON, E. B., and A. W. POLLISTER. 1937. Observations on sperm formation in the centrurid scorpions with special reference to the Golgi material. *J. Morph.*, 60: 407–443.

WORLEY, ELIZABETH K. 1939. A study of the sperm-forming components in three species of Decapoda. *Cellule*, 48: 147–176.

WORLEY, LEONARD G. 1943a. The structure and function of the Golgi system in the living cells of developing molluscs. *Proc. Nat. Acad. Sci. Wash.* 29: 225–228.

——. 1943b. The relation between the Golgi apparatus and "droplets" in cells stainable vitally with methylene blue. *Proc. Nat. Acad. Sci. Wash.*, 29: 228–231.

——. 1944a. Studies of the vitally stained Golgi apparatus. II. Yolk formation and pigment concentration in the mussel *Mytilus californianus* Conrad. *J. Morph.*, 75: 77–101.

——. 1944b. Studies of the vitally stained Golgi apparatus. III. The methylene blue technique and some of its implications. *J. Morph.*, 75: 261–289.

——, and E. K. WORLEY. 1943. Studies of the supravitally stained Golgi apparatus. I. Its cycle in the tectibranch mollusc *Navanax inermis* (Cooper). *J. Morph.*, 73: 365–399.

THE EFFECTS OF CHANGES IN CHROMOSOME NUMBER ON AMPHIBIAN DEVELOPMENT

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"Many of the phenomena dealt with here, like polyploidy, in spite of the fact that they are of great significance for the general theory of genetics, are at present almost completely ignored by zoologists, as the phenomena are largely peculiar to the plant kingdom." Preface, Sansome and Philp (1932).

INTRODUCTION

ONE of the characteristics that should be included in the description of every species of plant or animal is the number of chromosomes that are to be found in its cells. Normally, each species has a definite, constant number of chromosomes which is maintained through all the cell divisions of the long and complex processes of development. The process of mitosis itself is admirably constructed to assure an equal division of each chromosome and to send a complete and identical complement of chromosomes into the two daughter cells. It is during the formation of the reproductive cells of the mature organism alone that we find a modified form of mitosis which automatically and with perfect regularity brings about a reduction of the chromosome number to one-half. The mature egg and sperm both carry the reduced or haploid number to the process of fertilization, and the fusion of the two half-nuclei preceding the first cell division of the egg restores the full or diploid chromosome number of the species. The diploid chromosome complement thus consists of two haploid sets, one contributed by each parent.

In view of the fact that the chromosomes carry the great majority of the known hereditary factors, the maintenance of the specific chromosome number becomes an essential feature: it assures an equal share of both parents in inheritance and is a prerequisite for the normal functioning of heredity, which is based on the presence of two complete sets of hereditary factors or genes in each cell of the embryo. It is obvious that it would be of great importance to know what would happen if some natural or experimental accident should interfere with the normal chromosome cycle and bring about a change in the chromosome number in the cells of the developing embryo; for instance, if an extra set of chromosomes should be added at the time of fertilization so as to give to the embryo all the genes in triplicate. Such accidents do occur in nature, and they can also be induced experimentally in the laboratory. The consequences of the presence of more than two chromosome sets, a phenomenon known as polyploidy, have been investigated extensively in plants, where this condition is normally of frequent occurrence and easily induced by various experimental procedures.

Among animals, polyploidy is supposedly a rather rare phenomenon in nature. To be sure, we do not find many groups of races or species which constitute a polyploid series, i. e., which differ from one another in chromosome number by one or more haploid sets, as is so often the case in plants. However, recent investigations have shown that polyploid individuals do appear spontaneously and not infrequently in diploid species, and that polyploidy may be induced by simple treatments of eggs at the time of fertilization. As a matter of fact, among larvae of salamanders the frequency of spontaneous changes in chromosome number appears to be higher than in most diploid species of plants, and the percentage of polyploid individuals produced by treatments with cold or heat is considerably greater than that obtained in similar experiments with plants.

The neglect of this field by the zoologists may be attributed in part to the fact that work on polyploidy in animals, in striking contrast to corresponding studies on plants, offers little promise of immediate practical applications in animal breeding, or of important theoretical contributions to the study of the mechanisms of evolution. In addition, there has also been a lack of those convenient techniques for the ready identification of polyploid individuals in life that are so important to the plant geneticists. Significantly, interest in the effects of changes in chromosome number in animals arose from work in experimental embryology and developmental genetics.

There are many reasons why it soon appeared very desirable to develop a definite program for the study of polyploidy in animals. On the one hand, many aspects of polyploidy that have been thoroughly investigated in plants require a comparative study on animal material, since the conditions and consequences of such unusual changes in the genetic system are not the same in all details, in spite of the general validity of cytological and genetical principles for both plants and animals. Even if it were merely to complete the general picture, information on a number of problems should be gathered: (1) the occurrence and frequency of polyploidy in different groups of animals; (2) the origin of these exceptional individuals, in other words, the mechanisms that are responsible for their production; (3) the effectiveness of methods for the experimental induction of polyploidy; (4) the general effects of polyploidy on cell size, body size, and viability, and on the general physiology and biochemistry of the organism; (5) the occurrence of qualitative effects, which are added to the more obvious quantitative consequences.

In addition to these aspects of general biological significance there are many which are of special interest to zoologists or which are peculiar to animals, such as the influence of polyploidy on embryonic and later development, on growth rate and final body size, and on the structure and physiology of various organs and tissues,—in particular, the circulatory and nervous systems and the endocrine glands.

Finally, there is one phase in which for obvious reasons animals have already played a more important rôle than plants, namely, the influence of polyploidy on sex determination, although in recent years these results have been confirmed or extended in research on dioecious plants. Even here, the zoological information is limited to a few species, while a general understanding of the sex-determining mechanisms calls for a much wider basis including the vertebrates.

Among the latter, the most favorable material for a study of polyploidy that combines cytological and embryological investigations is without doubt furnished by the amphibians, and the salamanders in particular, for several reasons:

(1) They possess large cells and large chromosomes, which are counted with relative ease.

(2) The chromosome number may be determined in whole-mounts of tailtips clipped from living larvae soon after hatching, a rapid method which equals or surpasses the roottip method of plant geneticists.

(3) By means of pituitary stimulation it is possible to obtain viable eggs during the greater part of the year; the larvae are easily raised to advanced stages, in some species to sexual maturity.

(4) The development of the amphibian egg has been most thoroughly investigated by descriptive and experimental methods, so that it will be possible to combine, later on, methods of experimental embryology with studies on polyploidy.

(5) Since species hybrids are easily obtainable in amphibians in certain combinations, it should not be difficult to induce polyploidy in cross-fertilized eggs, a technique which has yielded highly important results in plants.

(6) The occurrence of occasional triploid embryos in preserved material has been demonstrated by various investigators in different species of frogs and salamanders.

Because of the diverse aims of the investigations on polyploidy in amphibians, some of the problems outlined above have not been attacked so far, and none of the aspects have been analysed with any degree of completeness. However, a considerable amount of information has accumulated and will be reviewed in this paper. Particular emphasis will be placed on the effects of polyploidy and of other changes in chromosome number on embryonic and larval development. Comparisons with polyploid invertebrates and plants will be drawn whenever they appear to be of particular interest. For more complete reviews of the work on polyploidy in plants the reader is referred to the articles listed in the first section of the bibliography.

TERMINOLOGY

The term *polyploidy* was introduced by Winkler in 1916 (p. 422) to designate individuals with three, four, or more complete sets of chromosomes in place of the usual two sets. At the same time he proposed the more general term *heteroploidy* to cover any deviation from the normal diploid chromosome number, whether by whole chromosome sets or by one or more single chromosomes. The latter term deserves wider use, since it is the only one that includes polyploidy and haploidy, as well as irregular chromosome numbers. To distinguish between the deviations that involve complete sets and therefore conserve the normal balance between individual chromosomes, and those that produce irregular or unbalanced chromosome combinations, Täckholm (1922) proposed the terms *euploidy* and *aneuploidy* which have been widely used by botanists.

A. METHODS OF IDENTIFYING LIVING HETEROPLOID INDIVIDUALS

1. Larvae

(a) Tailtip method

In many species of amphibians the fin surrounding the distal portion of the tail of the larva is thin enough to allow the preparation of whole-mounts in which the mitotic figures in the epidermis of the transparent fin may be studied with the oil immersion objective. Much of the classical work on mitosis was carried out on such preparations (Flemming, 1881–82, on *Salamandra*; Retzius, 1881, on *Triton*). Some of the first attempts to count the number of chromosomes were made on epithelial cells of the tailfin (Retzius, 1881). In the following year, Flemming (1882a) was able to determine the chromosome number in three cells of the buccal and gill epithelium of larvae of *Salamandra* as twenty-four but could not yet convince himself that this number might be constant for all the cells of the individual, and typical for the species.

The advantages of whole mounts of fin over sections of whole embryos or larvae for the determination of chromosome numbers were recognized early in the experiments on parthenogenesis, androgenesis, and related phenomena which produced haploid larvae (Bataillon, 1904; the Hertwigs, 1913; Levy, 1920a, b; Parmenter, 1933, 1940; and others). Either the chromosome number was determined directly by means of counts, or indirectly through measurements of the interphase nuclei, whose size increases roughly in proportion to the number of chromosomes which they contain. Later it was realized that portions of the tailfin, or the extreme tip of the tail itself, could be removed from living larvae, and their chromosome number determined while they proceeded with their development and, at the same time, regenerated the missing tissues (cf. Baltzer, 1922).

A simple method was thus available for the identification of the chromosome number of living amphibian larvae. All that was needed was to develop and apply it systematically to a large number of individuals in order to obtain information on the occurrence of spontaneous changes in chromosome number. The common Eastern newt, *Triturus viridescens*, was selected for the first investigations for three main reasons: (1) It offers considerable cytological advantages since the larvae have larger cells than those of many other species of salamanders, a thinner and more transparent tailfin with relatively few melanophores and little intra-epidermal pigment, and a diploid chromosome number of twenty-two (Fankhauser, 1932b) compared with twenty-four and twenty-eight in most other species. (2) The effects of haploidy had already been studied in this species by Kaylor (1937) in his experiments on androgenesis involving the removal of the maternal chromosomes in the second maturation spindle. (3) In preliminary experiments on androgenesis, two triploid embryos had been found among eleven preserved controls, demonstrating the not infrequent occurrence of exceptional polyploid individuals (Fankhauser and Kaylor, 1935).

The tailtip method was described in detail in an earlier paper in which the various evidences of polyploidy offered by the tailtip preparation were evaluated critically (Fankhauser, 1938c). Since then, the tailtip method has been applied successfully to several other species:

Triturus pyrrhogaster (2N = 24, fin less transparent because of more pigment; Fankhauser, Crotta, and Perrot, 1942).

Eurycea bislineata (2N = 28, smaller cells, fin less transparent because of thicker central layer of connective tissue, axis of the tailtip must be removed before mounting; Fankhauser, 1939).

Amblystoma mexicanum (axolotl, 2N = 28, smaller cells, more pigment except in larvae of the white or partial albino variety; Fankhauser and Humphrey, 1942).

Triturus torosus (Costello, 1942).

The summary of the technique given below applies to larvae of *Triturus viridescens* unless another species is mentioned.

The best stage for tail-clipping was found to be shortly after hatching (eighteen to twenty days at 20–22°C), when the fore limbs possess two prominent fingerbuds and show an indication of a third. At this stage, the yolk granules have disappeared from the epithelial cells of the tailfin; the number of mitotic figures is greater than in later stages (see Table 1); furthermore, several days elapse before the animals reach the feeding stage, so that it is possible to identify the heteroploid individuals in the meantime and to avoid wasting time feeding diploid larvae which are not to be kept as controls.

The larvae are anesthetized in a weak solution of chloretone (1:3000 to 1:5000); the posterior one-third (approximately) of the tail is amputated with fine scissors and dropped into Bouin's solution for from two to twenty-four hours. After a few hours in 70 per cent alcohol, the tailtip is stained in Harris' acid haemalum (diluted with 1 or 2 parts of water) for 3 to 4 minutes (depending on the age of the stain), washed for at least 20 minutes in several changes of tap water, dehydrated, cleared in xylene, and mounted in clarite (Fig. 4: 1–2).

The following criteria of changes in chromosome number may be used:

(1) Actual counts of chromosomes in epidermis cells at metaphase. Early metaphases usually present a polarview of the equatorial plate which is most satisfactory for counting (Fig. 4: 3–5). Later metaphases and anaphases are always seen in side view. If the original tailtip does not contain clear mitotic figures, as many as three additional tips with numerous mitotic figures may be obtained through regeneration from the same larva, at intervals of about two weeks (unpublished experiments of Rita C. Watson).

(2) Size of interphase nuclei. The nuclei of the epidermis are flat discs and show striking changes in size which are almost directly proportional to changes in chromosome number (Fig. 1). The nuclei of an unknown may be compared directly with those of a known diploid or triploid with the use of a comparison ocular. For more accurate study, twenty epidermis nuclei are drawn from the same region of each tailtip, and their total area is measured with a planimeter. Table 2 shows that this area increases rapidly between the haploid and triploid levels, but more slowly from there to the pentaploid level. The single measurement from a tetraploid individual is probably exceptionally large. In spite of considerable variations between individual tailtips, triploid larvae can be identified from such measurements if decisive chromosome counts should not be available.

In tailtips of axolotl larvae, the variations between nuclear measurements of individual tailtips with the same chromosome number are greater, so that there is considerable overlapping between the diploid and triploid ranges (Fankhauser and Humphrey, 1943, Table 1). Again, with higher chromosome numbers nuclear size increases more slowly. This may be explained in part by the fact that the thickness of the disc-shaped nuclei, as seen in optical section along the edge of the fin, remains practically constant up to the tetraploid chromosome number, but seems to show a slight increase in pentaploid cells (Fig. 3).

The nuclei of other tissues of the tailtip can also be used for comparison, although the differences between different levels of polyploidy are less striking in drawings of the largest optical sections through the nuclei because of their more rounded or oval shape (e. g., erythrocytes in capillaries of the fin, or in the small blood clot usually found at

TABLE 1

Number of metaphases in epidermis cells of tailtips amputated at different stages (approximately 24 hours apart). Twenty tailtip preparations of equal area were studied for each stage

STAGE	RANGE	AVERAGE
Third fingerbud indicated (F11)	1–21	12
Third fingerbud flat (F12) .	1–17	7.5
Third finger bud prominent (F13)	0–13	5.5
Larva begins to feed (F14) .	0–7	3
Later stages (development of 4th fingerbud, F15–F18)		2

Note: The number of mitoses does not seem to vary significantly during a 24-hour period, a fact which had already been stated by Retzius (1881), working with the tailfin of *Triton* larvae.

Early in this work it became obvious that the external features of the embryonic development of *Triturus viridescens* differ sufficiently in details from those of *Amblystoma punctatum* and *Triton taeniatus* to make the use of Harrison's stages or Glaesner's normal tables impractical. In the construction of our own normal tables, which consist of brief descriptions, the development was first divided into periods that are designated by capital letters (B for blastula, G for gastrula, N for neurula, E for the following "embryonic" period, F for the subsequent period characterized by the development of the forelimb buds, and H for the final period covering the formation of the hindlimbs). Each period is divided into a series of numbered stages (e. g., F0 to F18, H0 to H14).

Following H14, the stage marked by the presence of a well formed fifth toe, little external changes are visible, aside from growth, until the first signs of approaching metamorphosis appear. There are altogether sixty-five stages, not including the early cleavages, which are designated by cell number.

The embryology of *Triturus pyrrhogaster* was again found to be sufficiently different from that of *T. viridescens* to necessitate the compilation of a different table based on the same principles.

TABLE 2

Area, in square inches, of twenty epidermis nuclei from tailtips of larvae of Triturus viridescens, drawn at a magnification of 630 ×

	HAPLOID	DIPLOID	TRIPLOID	TETRAPLOID	PENTAPLOID
Chromosome number	11	22	33	44	55
Number of tailtips used for measurements	4	17	16	1	8
Area of nuclei					
range	1.52–2.38	3.95–5.29	5.95–8.94	11.5	8.62–11.75
average	2.0	4.65	7.0	11.5	10.0
ratio	1.00	2.32	3.5	(5.7)	5.0

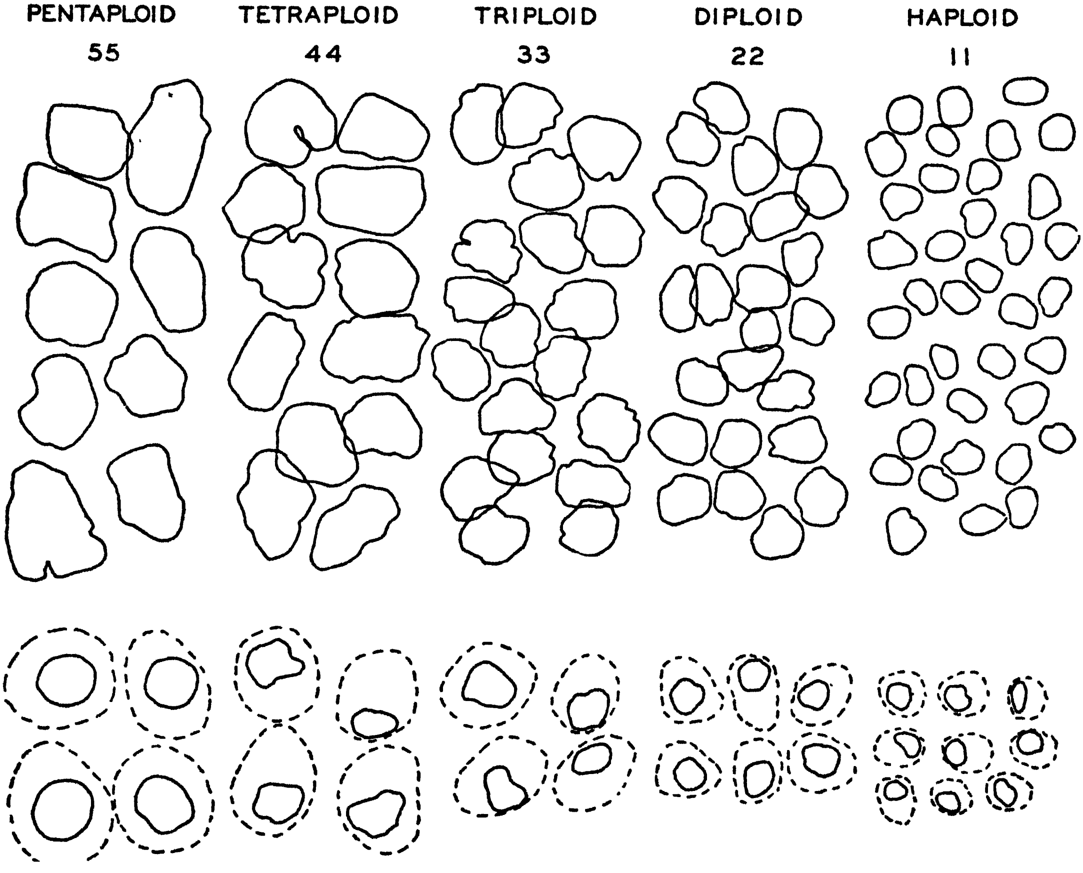

FIG. 1. RELATIVE SIZES OF NUCLEI AND CELLS FROM THE TAILFINS OF LARVAE OF TRITURUS VIRIDESCENS WITH DIFFERENT NUMBERS OF CHROMOSOME SETS

Above: Surface view of nuclei of epidermis cells. Nuclear size increases approximately in proportion to chromosome number. Below: Nuclei and cell boundaries of single gland cells (Leydig cells). Cell size increases with nuclear size. × 315.

the cut surface of the axis; nuclei of lateral line organs; muscle nuclei).

(3) The size of the cells, which is so useful in the detection of polyploid plants, cannot be used directly as a criterion because of the poor definition of the cell boundaries in most tissues. Exceptions are the erythrocytes and the gland cells (Leydig cells) in the epidermis (compare Fig. 1).

(4) Indirectly, the increased cell size is expressed in a wider spacing of the nuclei, which means a decrease in the number of nuclei per unit area. This is particularly obvious under the comparison ocular in the connective tissue layer of the fin (Fig. 4: 6–8).

(5) Since there is no significant increase in the body size of polyploid larvae, their organs are made up of a smaller number of larger cells. The decrease in number of cells or nuclei is often very plain in the lateral line sense organs (Fankhauser, Crotta, and Perrot, 1942, Figs. 7–8).

(6) In many species of plants, the number of nucleoli present in telophase or interphase nuclei is the same as the number of chromosome sets, since each nucleolus is formed at a localized region of a particular chromosome of each set ("nucleolar organizer"). The same relationship has been demonstrated in various species of animals, including amphibians (bibliography in Fankhauser and Humphrey, 1943). Among the salamanders studied so far, the species of *Amblystoma* are the only ones to show the nucleoli in the epidermal cells of the larval tailfin even without special staining methods, at least in some of the preparations. Although the numerical relationship is obscured in some of the nuclei through the fusion of nucleoli during interphase, the maximum number of nucleoli present always corresponds with the number of chromosome sets in the nucleus (Fankhauser and Humphrey, 1943, Figs. 1–8, Table 1). The value of this criterion is obvious, particularly in a species in which it is often difficult to obtain accurate chromosome counts.

Comparison of tailtip and roottip method: The tailtip of amphibian larvae has the great advantage of possessing a transparent fin, in which mitotic figures are accessible to the oil immersion objective in stained whole-mounts, without special treatment, while roottips cannot be used for chromosome counts without sectioning or smearing. Furthermore, while all the cells of the roottip are derived from one portion of the plant embryo, the radicle, the tailtip contains samples of cells from three widely separated regions of the amphibian embryo: most of the tissues originate from the material of the tailbud itself; the lateral line organs, however, grow out from a region behind the ear, and the blood cells originate in the blood island on the anterior ventral side of the embryo (cf. Fankhauser, 1938c, Fig. 6). Therefore, it is possible to test, in a single preparation, the chromosome condition of the embryo as a whole.

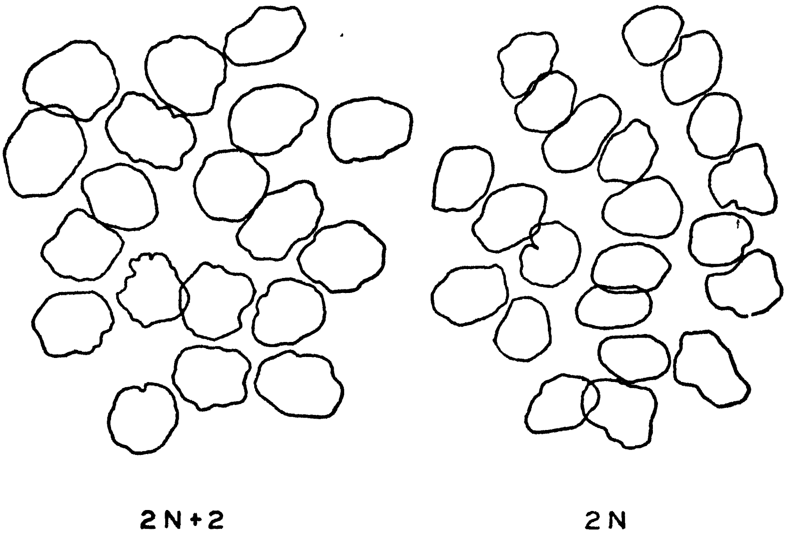

FIG. 2. NUCLEI OF EPIDERMIS CELLS FROM THE TAILFIN OF A HYPERDIPLOID LARVA OF TRITURUS VIRIDESCENS WITH 24 CHROMOSOMES (2N + 2) AND OF A NORMAL DIPLOID
Addition of two single chromosomes has caused a pronounced increase in nuclear size. × 315.

Detection of slight deviations in chromosome number. If the deviation from the normal chromosome number does not involve a whole set, actual chromosome counts are the only reliable means of identifying the heteroploid individual. However, a larva of *Triturus viridescens* with 24 chromosomes (2N + 2) was first discovered because of a considerable increase in the size of the epidermal nuclei of the tailfin (Fig. 2). It seems that in amphibians as well as in *Drosophila* (Dobzhansky, 1929) and in *Crepis* (Shkvarnikov, 1934) some individual chromosomes may exert a relatively greater influence on nuclear size than others. Among the salamander larvae, the presence of unbalanced chromosome complements has so far always been associated with conspicuous abnormalities in development that have aided in the identification of these aneuploid individuals.

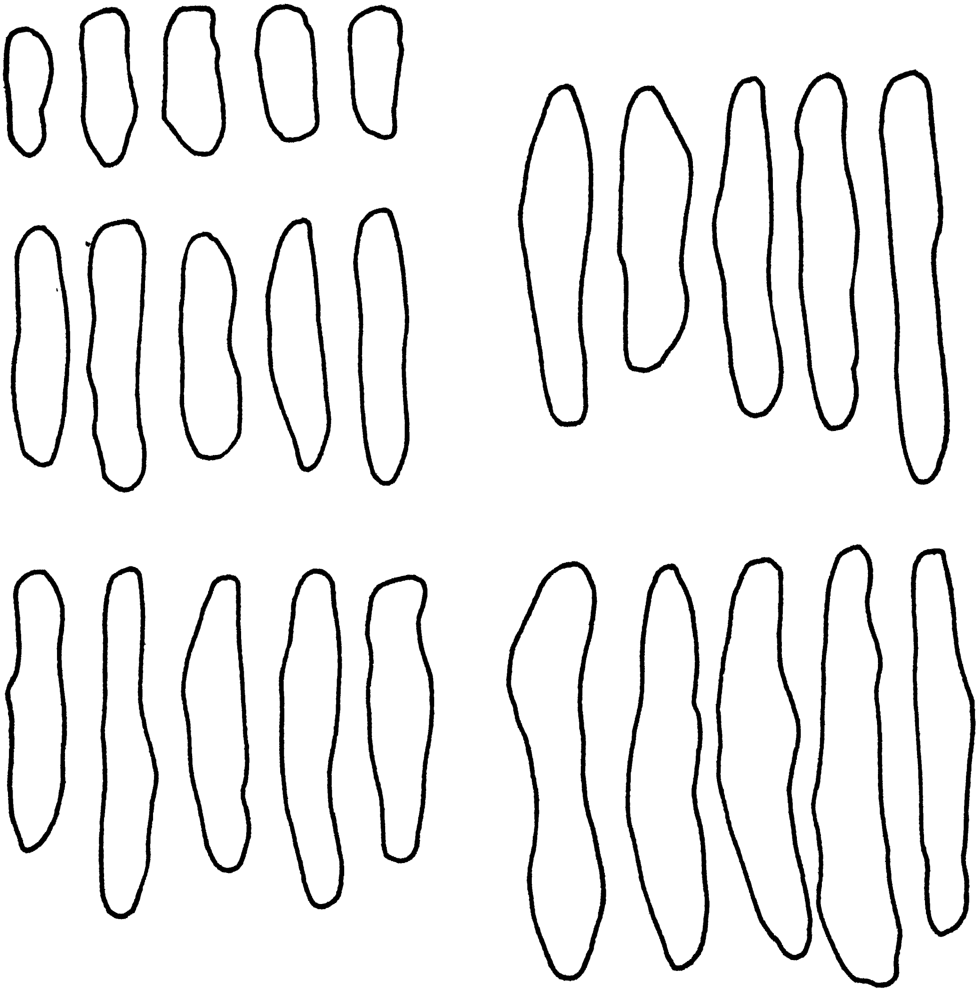

FIG. 3. OPTICAL SECTION THROUGH EPIDERMAL NUCLEI FROM EDGE OF TAILFINS OF AXOLOTL LARVAE
The nuclei are flat discs the thickness of which changes little with increasing chromosome number up to the tetraploid condition. On left: haploid, diploid, triploid. On right: tetraploid, pentaploid. × 1000.

(b) Pigment pattern of young larvae

The changes in cell size and cell number induced by deviations from the normal chromosome number are often clearly expressed in the pigment pattern of the young larvae. The size of the individual melanophores may be used as an index of the chromosome number in many cases, although the differences in size between diploid and triploid melanophores, for instance, may be obscured by differences in their state of "contraction" or "expansion," which varies considerably from day to day. It is therefore important to compare also the number of pigment cells present in certain

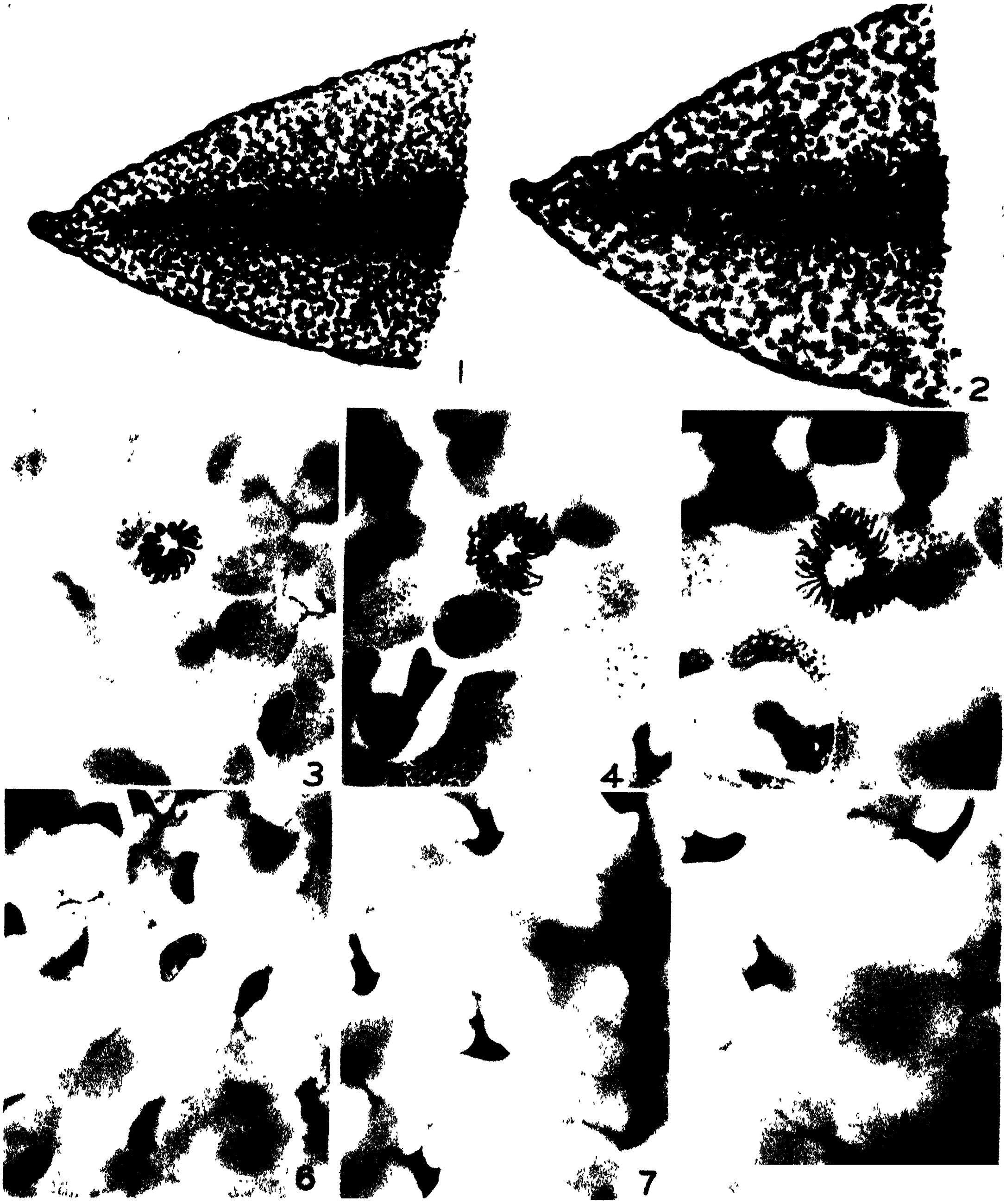

Fig. 4 Tailtip Preparations of Larvae of Triturus viridescens

1 Whole mount of tailtip of a diploid larva, stained with Harris' acid hemalum. Note transparent fin with large, pale epidermal nuclei and small, darkly stained, and irregularly shaped nuclei of mesenchymal cells. In the axis of the tail the spinal cord appears as a dark line, above it, on the dorsal side, a series of lateral line sense organs. × 50

2 Tailtip of a pentaploid larva. Nuclei and cells much larger. Cell boundaries not visible except in scattered gland cells near axis. Greater width of fin seems to be typical of pentaploid larvae. × 50

3 to 5 Metaphases in epidermis cells in tailfins of diploid, triploid, and pentaploid larvae. The chromosomes are too long and too crowded to be counted in photographs. × 392

6 to 8 Left to right. Connective tissue cells, from the mesenchymal layer supporting the tailfin, from a diploid, a triploid, and a pentaploid larva, respectively. The size and spacing of the nuclei increases with the chromosome number. The branching cytoplasmic processes, however, do not show any appreciable change in thickness. × 392

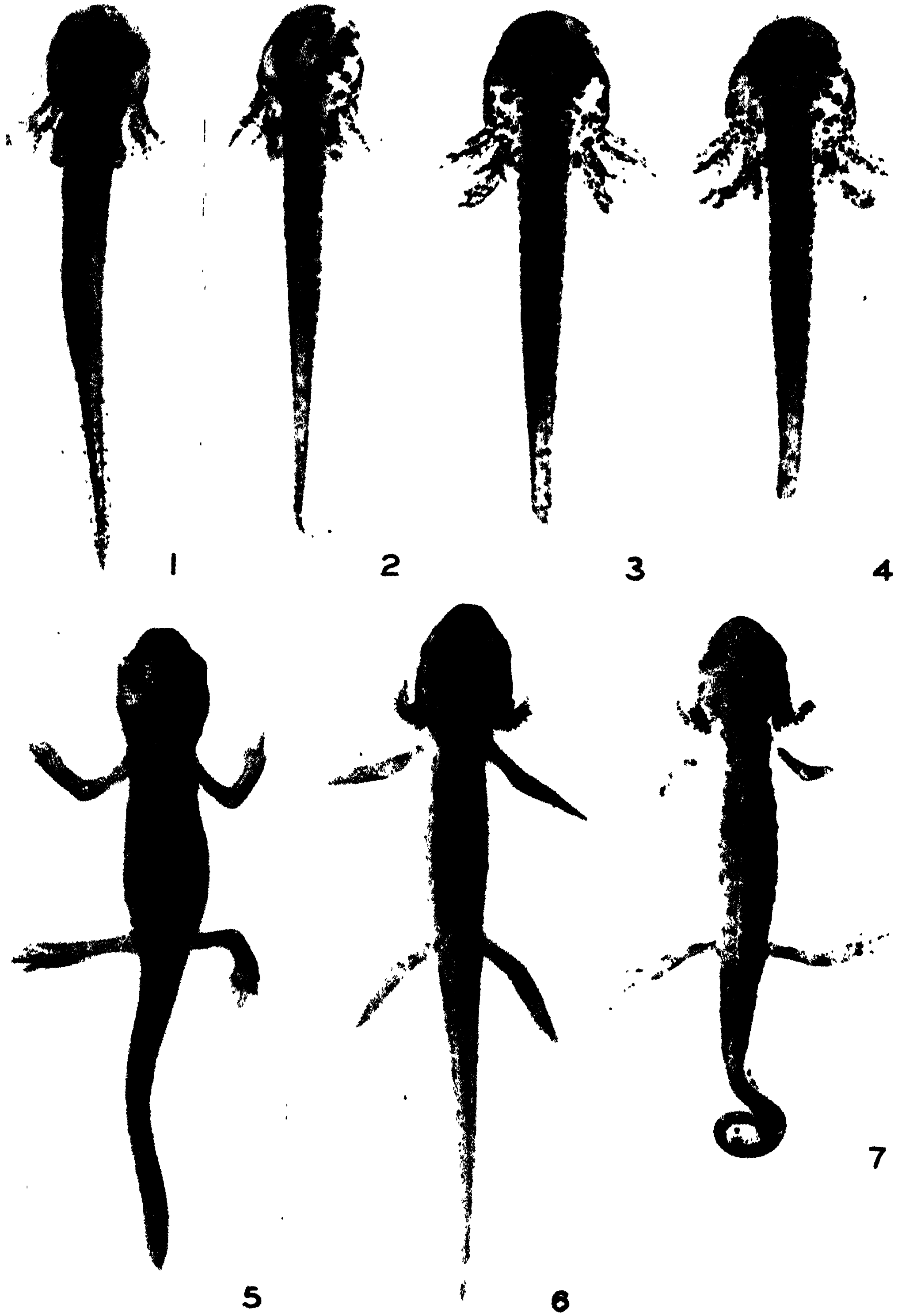

Fig. 5

areas like the head, the flank, and the tailfin. Since the body size of the larvae remains fairly constant at different levels of polyploidy, there are noticeably fewer pigment cells in the polyploids, in unit areas, than in the corresponding areas of diploids (Fig. 5: 1–4). In haploid larvae, on the other hand, although they are usually smaller from an early stage on, the increase in the number of melanophores per unit area is still very noticeable (Fig 7).

In practice, all larvae are examined and classified with regard to their pigment pattern as early as possible All suspicious looking animals are then tail-clipped for a cytological check, the result of which very often agrees with the prediction; of the larvae with unmistakably diploid pigment pattern only a small number are tail-clipped to furnish control preparations for comparison.

2. *Metamorphosed and adult salamanders*

In the laboratory, triploid salamander larvae have been found to be as viable as diploids in *Triturus viridescens* and *T pyrrhogaster* Since they occur spontaneously with considerable frequency (see Table 3) some of these, at least, should grow to adult size under natural conditions Up to the present, a single adult triploid has been discovered, a male newt (*Triton taeniatus*) found by Book (1940) in Sweden In a large collection of testes fixed for a reexamination of spermatogenesis, one pair contained triploid spermatogonia and, during various stages of meiosis, showed the typical irregularities of triploid organisms The body of the animal had not been preserved, presumably it was triploid throughout

Polyploid adults might be detected in life by the following methods. (1) determination of nuclear and cell size in pieces of shed skin, (2) determination of nuclear size, and perhaps chromosome counts, in sections or in whole mounts of epidermis from the amputated tip of the tail, and, later, from the regenerating tailtip; (3) measurements of the size of erythrocytes in blood smears made at the time of amputation.

The last-mentioned method was put to a preliminary test by Michalski (1942) with large larvae and adults of *Eurycea bislineata*. The blood samples were diluted with physiological salt solution and studied immediately under a cover glass ringed with vaseline The living erythrocytes vary from 32 to 37 micra in length, with an average of 33 4 micra, and from 19 to 21 micra in breadth, with an average of 20 micra. Of 117 animals studied, all possessed red blood cells within the normal range of variation of diploid individuals and were therefore presumably all diploid.

In tailtip preparations of newly hatched *Eurycea* larvae the nuclei and cell bodies of erythrocytes are strikingly larger in triploids (Fankhauser, 1939, Fig 18). In young axolotl larvae, the erythrocyte nuclei of triploids average 15 micra in length, compared with 12 7 micra in diploids (Fankhauser and Humphrey, 1942). It should thus be possible to identify triploids among adults, unless the initial difference in cell size is reduced in the adult through a process of regulation

B. ADDITION OR SUBTRACTION OF WHOLE CHROMOSOME SETS (POLYPLOIDY AND HAPLOIDY)

1 *Frequency of spontaneous aberrations*

Earlier occasional observations by several investigators indicated that triploid individuals occur not infrequently among normal embryos raised from eggs that were not subjected to any experimental treatment (G and P Hertwig, 1920, *Rana esculenta*, Dalcq, 1930, *Rana fusca*, *R. esculenta*, Fankhauser, 1934c, *Triton palmatus*, Fankhauser and Kaylor, 1935, *Triturus viridescens*, cf. Fankhauser, 1938c, Table 1). These exceptional embryos were identified after fixation by chromosome counts in sections Unless the

FIG. 5. TRIPLOID AND TETRAPLOID LARVAE OF TRITURUS VIRIDESCENS AND CONTROLS

1 and 2. Young diploid (left) and triploid larvae after precocious removal from jelly capsules (stage F8, forelimb buds notched, several days before tailclipping) The presence of larger but fewer pigment cells (melanophores) on the head is the earliest visible criterion of triploidy × 10

3 and 4 The same larvae one week later, after removal of tailtips (stage F12, flat third finger bud). Maximal expansion of menalophores, which partly obscures the difference in pigment pattern × 10

5 and 6. The same animals at the age of about 3 months. The diploid has completed metamorphosis and left the water. note blunt snout, bulging eyes, almost complete disappearance of gills, black pigment spots formed by clusters of melanophores, few white pigment spots on left side of body which turn vermilion later on The triploid, slightly longer, is entering metamorphosis (first molt layer shed in part, black spots forming, gills slightly reduced, eyes beginning to bulge, snout still larval in shape). × 3.

7: Tetraploid larva (the only one found so far in this species) at metamorphosis, 4½ months old Body size approximately normal. Single melanophores scattered between black spots clearly larger than in 6. Coiling of tail and pointed snout appear to be typical for animals with more than three sets of chromosomes. × 3

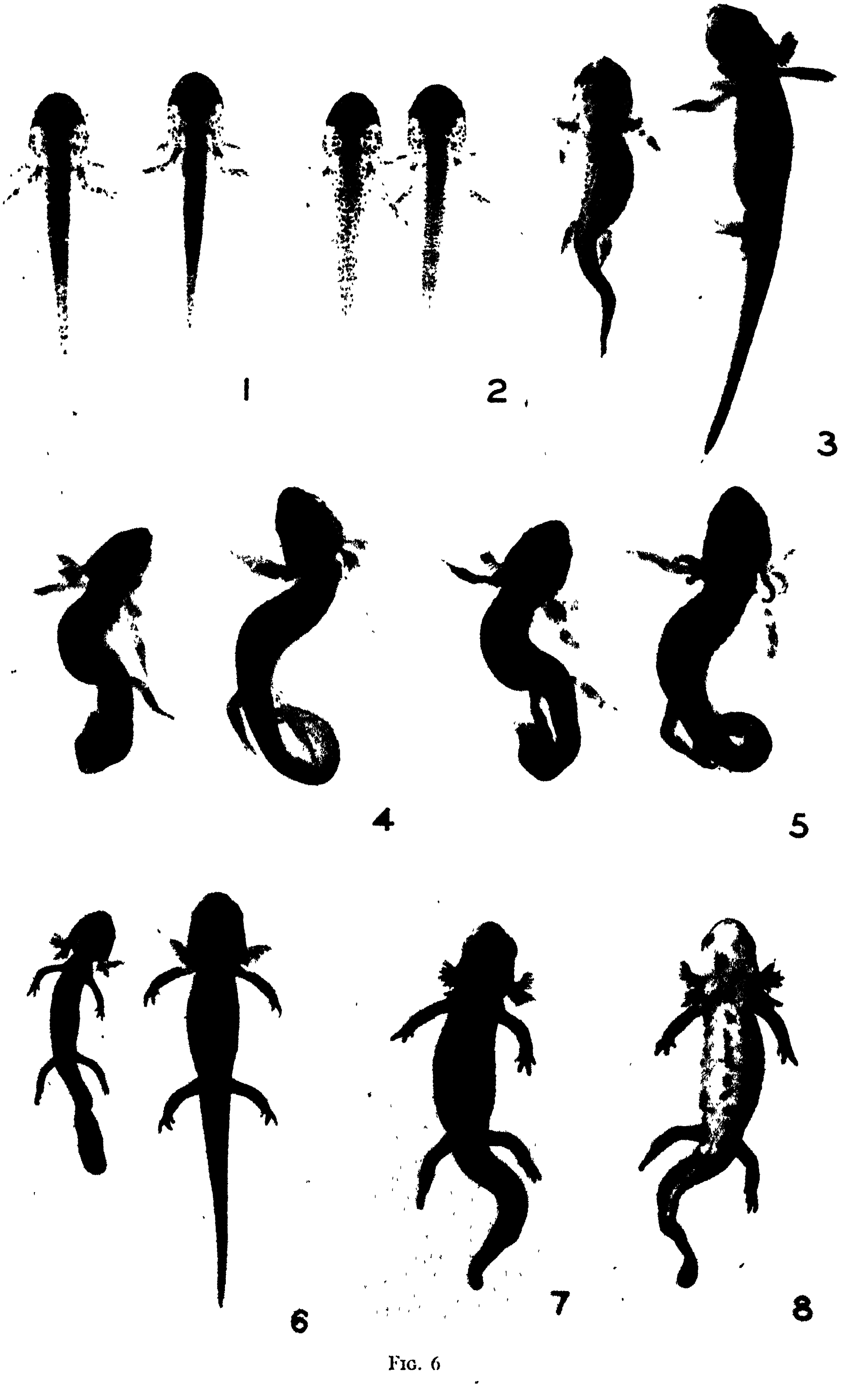

FIG. 6

viability of the embryos is greatly decreased by the deviation in chromosome number, such exceptional individuals should still be present among the young larvae at the time of hatching, when they may be identified in life by the tailtip method described earlier.

Beginning in November 1937, a systematic search for exceptional heteroploid individuals among young larvae of *Triturus viridescens* has been carried out, with the collaboration of several graduate and undergraduate students. While the normal breeding period is in the spring, egg-laying may be induced from late October on by implantation of two anterior lobes of frog pituitary, given two days apart (Kaylor, 1937). On the approach of the normal breeding season, the dose may be decreased to one or one-half a lobe to avoid overstimulation and deposition of large numbers of unfertilized eggs on the bottom of the culture dish. Since the adult females usually carry a store of spermatozoa in the spermatheca from the fall mating season, the eggs are fertilized in normal fashion as they are laid singly on leaves of *Elodea*. Eggs which are attached to the bottom of the aquarium very rarely are fertilized.

Since the time of the last detailed report (Fankhauser, 1941b), the total number of larvae that have been classified with regard to chromosome number has been more than doubled (Table 3). From the outset of these observations it appeared that triploidy is the predominating type of spontaneous heteroploidy, occurring with the relatively high frequency of 1.8%. This percentage varies greatly with different matings and may thus be influenced by genetic factors, the highest proportion of triploids produced by any female was eight among a total of 29 larvae, or 27.6 per cent (unpublished observations of W. T. Powers).

It was expected that tetraploid larvae would occupy the second place in frequency; however, only a single tetraploid larva has been found so far, as contrasted with seven pentaploids (0.28%). It is interesting to note that in January, 1943, two pentaploid larvae were obtained from a group of 34 untreated eggs laid by one female during one day.

In view of the numerous experiments on the induction of haploid development in amphibian eggs of various species, carried out by many investigators during the past thirty years, as well as the striking appearance of the haploid larvae, it is surprising that spontaneous haploids were not discovered until 1940/41, when they first appeared among larvae of three species of salamanders, *Triturus viridescens*, *Triturus pyrrhogaster*, and *Eurycea bislineata* (a lungless salamander of the family Plethodontidae). Since then more haploid larvae have been found in the first mentioned species and also among larvae of the axolotl.

Compared with deviations involving whole chromosome sets, aneuploid or unbalanced aberrations adding or subtracting one or more single chromosomes seem to be rare. Only two such larvae have been discovered so far in *Triturus viridescens*. The actual frequency of embryos with aneuploid chromosome complements may be considerably higher, for two main reasons: (1) slight deviations in chromosome number cannot be discovered as a rule except by counts in particularly clear metaphase plates that are free from crowding and overlapping of chromosomes; and (2) the disturbance of the genic balance in aneuploids may lead to abnormal development and death at an early embryonic stage, long before the tailtip test can be applied; actually, both the hyperdiploid and the hypo-diploid larva were strikingly abnormal and unviable.

FIG. 6. PENTAPLOID ANIMALS AND CONTROLS

1. Pentaploid (left) and diploid larvae of *Triturus viridescens*, 3½ weeks old (stage F17, flat fourth finger bud), 5 days after amputation of tailtips. Melanophores contracted. Pentaploid normal except for pigment pattern and slightly larger size. × 4.5.

2. Same animals, 5½ weeks old (stage HO, first appearance of hindlimb buds). Body cavity of pentaploid extended with fluid (ascites). Melanophores expanded. × 4.5.

3: Another pentaploid larva (left) approaching metamorphosis, 4½ months old, with a triploid animal in a similar stage. Note small size, S-shaped curvature of body axis, and pointed head of pentaploid. × 1.8.

4: Two other pentaploid larvae at age of 102 days, approaching metamorphosis. Animal on right nearly normal in size. Both show strong curvature of body axis and coiling of tail. × 2.1.

5. The same two pentaploids 8 days later. The animal on right has shed the first molt layer, gill branches and tailfin much reduced. All external metamorphic changes normal, including formation of black and white (later vermilion) pigment spots. × 2.1.

6: Pentaploid (left) and diploid larvae of *Triturus pyrrhogaster* at the age of 3 months, showing difference in growth rate. The diploid larva entered metamorphosis shortly afterwards. Body axis of pentaploid shows slight curvature. × 1.6.

7 and 8: Dorsal and ventral views of the same pentaploid as in 6, at age of 4¾ months. Beginning of metamorphosis (one day before first molt). The animal has reached approximately normal body size and shows a more pronounced curvature of tail. × 1.6.

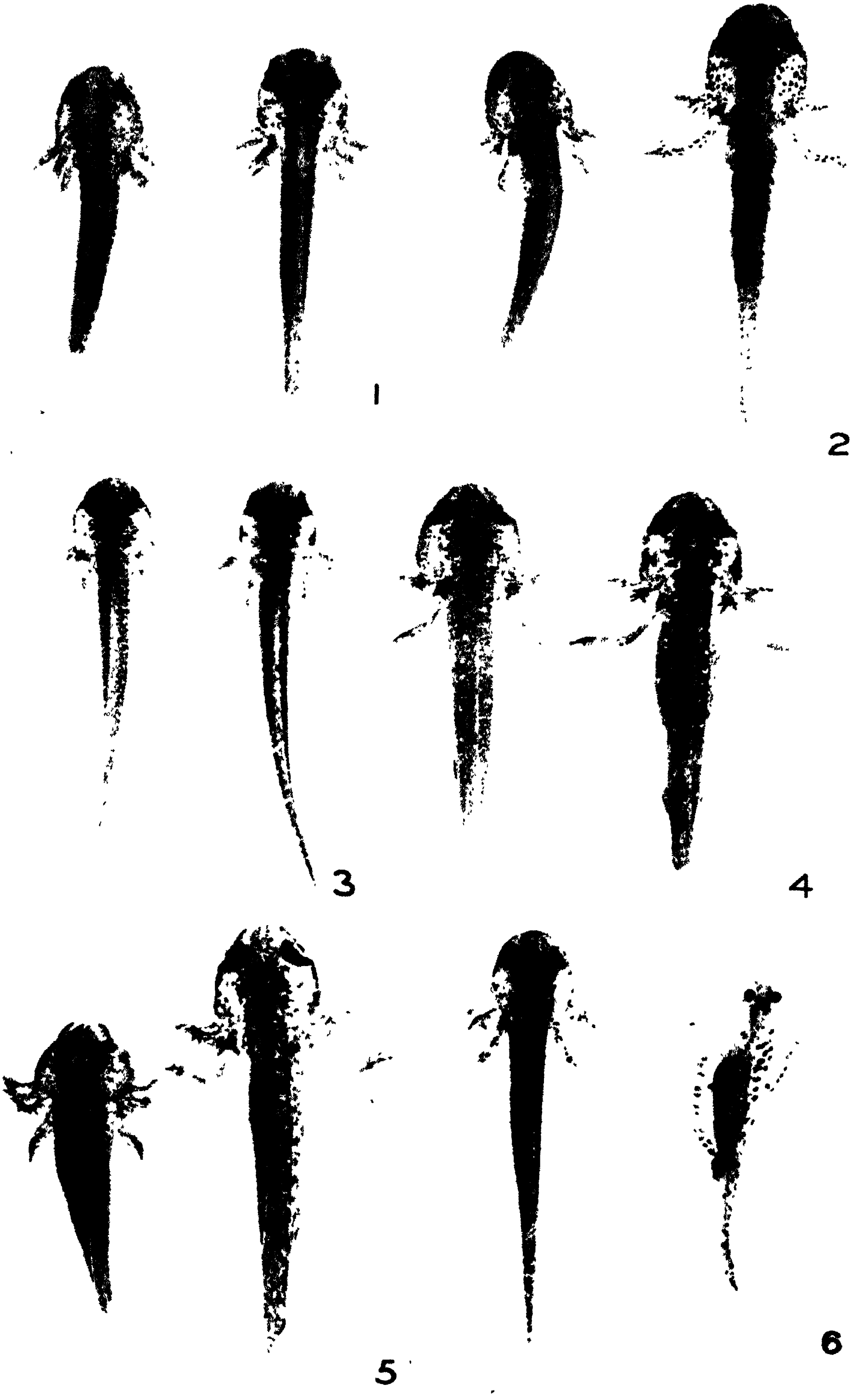

Fig. 7

A third group of rare aberrations includes chromosome mosaics, larvae in which different chromosome numbers, e. g., haploid and diploid, are present in different parts of the body. Haploid and diploid cells may be equally abundant, or one type may predominate; they may show a bilateral distribution with a clear line of demarkation coinciding for the greater part with the median plane of the larva, or they may be irregularly mixed so that most of the organs are composed of both types of cells. Again this type is probably more frequent than would appear from Table 3, since in most cases they are discovered only when the tip of the tail itself has a mosaic constitution. When the cells of one chromosome constitution are more numerous than those of the other, the condition is not recognized, as a rule, except by a careful study of sections through the preserved animal.

TABLE 3

Frequency of spontaneous changes in chromosome number among young larvae of four species of salamanders

	TRITURUS VIRIDESCENS (2N = 22) NOV. '37–JUNE '44	TRITURUS PYRRHOGASTER (2N = 24) 1940/41, '44	EURYCEA BISLINEATA (2N = 28) 1938/39, '40/42	AXOLOTL (2N = 28) 1942–44
Total number of larvae examined	2448	398	546	over 3000
Diploid	2387	392	511	
Triploid	44 (1.8%)	4 (1%)	28 (5.1%)	1
Tetraploid	1	—	2	1
Pentaploid	7 (0.28%)	1	—	2
Haploid	4 (0.16%)	1	2	7
Hyper-diploid (2N-2)	1	—	—	—
Hypo-diploid (2N-3)	1	—	—	—
Mosaics:				
haploid/diploid	1	—	3	2
haploid/triploid	1	—	—	—
diploid/hyper-triploid	1	—	—	—

Less extensive investigations on the occurrence of spontaneous polyploidy have been carried out on larvae of the Japanese newt, *Triturus pyrrhogaster* (Fankhauser, Crotta, and Perrot, 1942; and unpublished observations made in 1944), and of the two-lined salamander, *Eurycea bislineata*. In the former, the frequency of spontaneous triploidy seems to be similar to that in *Triturus viridescens*. In *Eurycea bislineata* it is considerably higher, although not as high as was indicated by the first observations that demonstrated the existence of 13 triploids and 2 tetraploids among 134 larvae (Fankhauser, 1939). Later, Michalski (1942) identified 15 triploids, 2 haploids, and 3 haploid/diploid mosaics among 412 larvae. As in *Triturus viridescens*, the proportion of triploid larvae produced varies with different females; perhaps it is also influenced by other, as yet unknown conditions.

In 1942, the investigations on polyploidy were

FIG. 7. HAPLOID LARVAE AND CONTROLS; HYPER-DIPLOID LARVA

1: Spontaneous haploid larva (left) of *Triturus viridescens*, developed from an untreated egg, and a diploid at the same stage of development (F12, flat third finger bud). Haploid 3 weeks old, diploid slightly younger. Haploid slightly shorter (appears much shorter because of removal of a larger portion of tail than in diploid). Pigment cells smaller and more numerous, eyes smaller. × 7.

2: The same animals 2 weeks later. The haploid (left) has reached the final stage of its development. It has fed little, shows reduction of gills, fusion of digits, increasing curvature of body, and mild ascites. × 7.

3: Haploid larva (left) of *Triturus pyrrhogaster*, developed from a refrigerated egg, and control, 18 days old, before amputation of tailtips. Haploid easily identified by small, numerous melanophores. × 5.6.

4: The same larvae, 39 days old, shortly after second amputation of tail. The haploid (left) is practically normal in size and general appearance, except for the pigment pattern. It had previously fed well but suddenly refused all food and was preserved five days later. × 5.6.

5: Another cold-induced haploid larva (left) of *Triturus pyrrhogaster* and its control, 31 days old. The haploid shows the characteristics of most haploid amphibian larvae: dwarfing, edema, microcephaly. It never fed. × 5.6.

6: Highly abnormal hyper-diploid larva (right) of *Triturus pyrrhogaster* (27 or 28 chromosomes = 2N + 3 or 4) and control of same age. Extreme microcephaly and edema are the most striking features. × 5.

extended to axolotl larvae, in collaboration with R. R. Humphrey of the University of Buffalo. The primary aim of this line of work has been the experimental induction of triploidy in combination with breeding experiments, and the analysis of the influence of triploidy on sex. No systematic check of all untreated larvae for the presence of aberrant chromosome complements was attempted, except in the first series of experiments where a single triploid was found among 148 larvae (Fankhauser and Humphrey, 1942). The other heteroploid larvae listed in Table 3 were picked out from a large number of controls because of their striking appearance, particularly with regard to the pigment pattern. This accounts for the absence of additional spontaneous triploids, since the differences in pigment pattern between triploid and diploid larvae are rather slight in this species, so that experimentally induced triploids often remain unidentified until the tailtip preparations have been studied.

Possible influence of pituitary-induced ovulation on the frequency of heteroploidy

With the exception of the axolotl, most of the observations listed in Table 3 were made on material obtained by pituitary stimulation of the females. The artificially induced ovulation might conceivably be responsible, at least in part, for the frequent production of abnormal chromosome numbers. However, it can be shown that aberrations occur with approximately equal frequency during the winter and during the normal breeding season, in spite of the difference in the amount of stimulation required to produce egg-laying. Furthermore, heteroploid larvae have been obtained from eggs of *Triturus viridescens* laid in the laboratory by unstimulated females. This, of course, does not prove conclusively that populations of young larvae collected in their natural habitat contain as high a proportion of individuals with abnormal chromosome numbers. This necessary test cannot be carried out with larvae of *Triturus viridescens*, since the eggs of this species are laid singly on water plants and the chances are slight that any number of eggs or young larvae could be collected. With other species which deposit the eggs in batches, such as *Amblystoma* and *Eurycea*, the test should not be difficult.

Comparison with other animals and with plants

No accurate figures are available for the frequency with which occasional polyploid individuals appear in other species of animals. In *Drosophila*, Morgan, Bridges, and Sturtevant (1925, p. 161) stress the "very high frequency for the occurrence of triploidy." This statement is based on the fact that within five years from their discovery in 1920 "intersexes of the triploid type have been found 15 times and there have been seven discoveries of triploid females originating de novo from diploid lines." However, the total number of individuals classified during this period must have been very large, and more recent rough estimates made by several *Drosophila* workers in personal conversation put the actual frequency of triploidy well below one per cent. We do know, however, that a completely haploid *Drosophila* has not been seen yet, although a number of haploid/diploid mosaics are on record.

In plants, the frequency with which polyploid and haploid individuals appear spontaneously has been recorded in relatively few cases only. The figures that have come to my attention are listed in Table 4; a wider search of the literature would undoubtedly produce others. A glance at the table shows that, in the majority of species, triploids appear with a frequency considerably below one per cent. The frequency is increased when one or both of the parents are trisomic, i. e., when they carry an extra chromosome. An exceptional case has been recorded by Shull (1929) in *Oenothera* where 12 per cent triploids appeared in one family. The cause of this unusual behavior could be traced to the mother, which produced an unusually high proportion of unreduced eggs. The proportion of spontaneous haploids in maize, in the jimson weed, *Datura*, and in the snap-dragon, *Antirrhinum*, the three species in which the most extensive counts were made, is one in 2000 or lower. Compared with these frequencies in plants, heteroploid salamander larvae occur with impressive abundance.

2. *The origin of spontaneous aberrations in chromosome number*

(a) Triploidy

Triploid individuals arise through the union of an unreduced, diploid gamete with a normal, haploid one. The third chromosome set may thus be contributed by either parent. If the parents differ in genetic constitution, the appearance of the triploid offspring may tell where the additional chromosome set came from. In plants it seems to be furnished usually by the egg, perhaps for the very simple reason that the pollen tubes produced by diploid pollen grains often burst when growing in a normal, diploid style. In the one clearly established case of paternal origin of the extra chromosome set, in maize (Rhoades, 1936), it seems more likely that two haploid sperm nuclei, rather than a single, diploid nucleus, fused with a haploid egg nucleus (dispermy).

TABLE 4

Frequency of spontaneous polyploidy and haploidy in plants

SPECIES	AUTHOR	CHROMOSOME NUMBER	FREQUENCY	REMARKS
Maize	Einset, 1942, 1944b	triploid	3 in 1916	Offspring from cross between trisomic and diploid plants
		haploid	2 in 1916	
	Randolph, 1941	haploid	ca. 1 in 2000	
	Randolph and Fischer, 1939	parthenogenetic diploid	23 in 17,165 (ca. 1 in 750)	in tetraploid race
Datura	Satina, Blakeslee, and Avery, 1937	haploid	73 in ca. 410,000 (0.018%)	
Antirrhinum majus	Knapp, 1939	haploid	ca. 1 in 2000	
Tomato	Lesley and Lesley, 1930	triploid	3 in ca. 9000	from diploid parents
			6 in ca. 2000	from trisomic parents
Cucumis	Shifriss, 1942	tetraploid	1 in ca. 25,000	
		parthenogenetic diploid	8 in 800	in tetraploid race
Apple	Einset, 1944a	triploid	2 in 278	in a much larger population the frequency has since been found to be lower (Einset, 1944b)
		tetraploid	1 in 278	
Crepis capillaris	Navashin, 1925	triploid	1 in 150	Sudden rise in temperature suggested as cause of relatively high frequency
		pentaploid	1 in 150	
Oenothera	Shull, 1929	triploid	19 in 148 (12%)	in one family only; the average frequency is considerably lower

In triploid animals, genetic criteria have not been available so far to decide directly the question of their origin. However, some evidence has been furnished by experiments on cross-fertilization between different species of frogs and toads in which the penetration of the foreign spermatozoon stimulates the egg to divide but the sperm nucleus does not take part in development ("gynogenesis"). Such eggs give rise to "false hybrids" that are usually haploid; occasionally, however, diploid larvae of purely maternal character appear which must have developed from diploid eggs (G. Hertwig, 1918, etc.; Tchou-Su, 1931, 1936). One female of *Rana esculenta*, when crossed with a male *Bufo viridis*, produced false hybrids which were all diploid; eggs of the same female fertilized by sperm of its own species gave rise to triploid tadpoles (G. and P. Hertwig, 1920). Tchou-Su (1936) showed that, in crosses between Chinese species of anurans, diploid false hybrids develop from eggs which did not give off the second polar body. On the other hand, Bataillon and Tchou-Su (1929, fig. 24) described an unfertilized egg of *Bufo calamita* in which the second maturation spindle contained the diploid number of dyads.

Unreduced gametes of either type may originate in various ways, primarily (1) from tetraploid oocytes or spermatocytes in animals, from tetraploid mega- or microsporocytes in plants, through normal meiosis, and (2) through disturbances of meiosis in normal, diploid cells.

(1) The literature contains numerous reports on the occurrence of groups of tetraploid cells in the first meiotic division, or in pre-meiotic divisions, in diploid plants and animals, including man (Painter, 1923). Sometimes polyploid germ cells occur with surprising frequency, as in the grasshopper, *Rhomalea microptera*, where Mickey (1942a, b) found cells showing various degrees of polyploidy in each follicle studied. A similar condition observed in barley has been traced to the presence of a recessive factor which causes the formation of a variable proportion of "multiploid" microsporocytes (L. Smith, 1942).

In amphibians, tetraploid cells have been seen in the testis of frogs (Levy, 1920a). A preliminary study of testes of *Triturus viridescens* and *Eurycea bislineata* has demonstrated so far the existence of a few giant, presumably tetraploid, spermatocytes in a single testis of the first mentioned species. It seems clear that diploid spermatozoa could not be produced in this way in sufficient number to account for the occurrence of almost two per cent triploid larvae. An instance of normal maturation of a tetraploid oocyte is probably given by the diploid egg of *Bufo calamita* mentioned above. More information on the chromosome number of ovarian eggs should be obtainable by counting the bivalents in isolated germinal vesicles.

(2) Disturbances of meiosis in diploid cells (failure of synapsis, suppression of the first or second maturation division) leading to the formation of diploid gametes in animals and diploid spores in plants have been described frequently. In amphibians, diploid eggs are formed occasionally through suppression of the second maturation division, as is shown by Tchou-Su's observations mentioned earlier. That triploid embryos may originate spontaneously in this way is also indicated by the fact that triploidy may be easily induced by cold or heat treatment of salamander eggs during the second maturation division.

(b) Tetraploidy

Tetraploid zygotes may result from the chance meeting of an exceptional unreduced egg and an exceptional unreduced sperm, an accident which should be very rare. In *Drosophila*, fertilization of a triploid egg by a haploid sperm has been suggested as a possible origin of the rare tetraploid females, because hexaploid sectors have actually been seen in gonads of triploid individuals from which triploid eggs should arise by normal meiosis.

In the silkworm, *Bombyx*, genetic evidence indicates that tetraploid females may originate by fertilization of triploid eggs by haploid spermatozoa; in this species, however, the triploid condition of the eggs seems to be derived from the fusion of the egg nucleus with two haploid polar nuclei, rather than by normal maturation of hexaploid oocytes (Hasimoto, 1934).

Doubling of the diploid chromosome number during the first division of the zygote, following normal fertilization, would also produce tetraploid embryos ("somatic doubling"). Evidence concerning the relative importance of these various possibilities in the production of the rare spontaneous tetraploids among salamander larvae is lacking.

(c) Pentaploidy

The formation of pentaploid zygotes can be interpreted most easily as the result of a fusion between a tetraploid and a haploid gamete. A tetraploid gamete may originate in various ways, e. g., by suppression of both maturation divisions and inclusion of all tetrads in a single nucleus, or by suppression of the second maturation division in a cell which was already tetraploid at the beginning of meiosis. Navashin (1925) suggested suppression of both maturation divisions, producing a tetraploid gamete, as the most probable origin of his pentaploid individual of *Crepis capillaris*. The predominance of individuals with odd numbers of chromosome sets among salamander larvae, compared with the scarcity of tetraploids, clearly shows that accidents leading to changes in chromosome number happen much more frequently during meiosis than during the early divisions of the zygote.

(d) Haploidy

The great majority of haploid plants are purely maternal in appearance and therefore parthenogenetic in origin. Paternal, androgenetic haploids do occur, however. In *Antirrhinum*, for instance, Knapp (1939) found a ratio of 0.05 per cent maternal haploids to 0.005 per cent paternal ones.

During the past year observations on haploid axolotl larvae derived from crosses between genetically different races have produced some evidence regarding their mode of origin (Humphrey and Fankhauser, unpublished). A mating between a homozygous dark female and a recessive white male produced one haploid larva which was white and must therefore have developed with a paternal set of chromosomes, i. e., by androgenesis. Other matings have indicated, although less conclusively, that haploid embryos may also originate by gynogenesis, or possibly parthenogenesis. Additional information from black by white crosses should tell soon which of the two types of accident leading to haploidy is actually more common.

(e) The possible rôle of polyspermy

Polyspermy, which was mentioned as the mechanism producing triploidy in maize in one case, may also be involved in salamanders, where it is actually a natural or "physiological" phenomenon. However, the supernumerary spermatozoa present in the majority of the eggs are effectively prevented from taking part in development, so long as their number remains small (Fankhauser, 1932a; Fankhauser and Moore, 1941a). The maximum number tolerated by the egg, and the stage to which the accessory spermatozoa develop before degenerating vary considerably between different species. In spite of the existence of an inhibiting mechanism, it is not improbable that an extra set of chromosomes may be contributed by an accessory sperm nucleus in rare cases.

3. *Experimental induction of changes in chromosome number*

In spite of the relatively high frequency with which heteroploid salamander larvae appear spontaneously, it would take many years to collect enough information on the influence of various abnormal chromosome complements on development. Obviously it would be very useful to have methods by means of which some types of heteroploidy could be induced experimentally, similar to the procedures that have been used by plant geneticists in recent years with so much success. Among zoologists interest in such techniques was limited for a long time to those inducing haploidy, since this whole line of investigation began with the classical experiments on parthenogenesis with eggs of frogs, which were followed by studies on gynogenesis, androgenesis, and merogony in amphibians in general. All these modifications of the normal process of fertilization typically lead to the formation of haploid embryos, although other deviations in chromosome number, including polyploidy, may be obtained as occasional by-products whose origin is usually unknown. It was not until 1939 that the experimental addition of a third chromosome set to the normal diploid complement became possible, while the problem of inducing higher levels of polyploidy in amphibian eggs has not been solved at present.

(a) Haploidy

The various methods that may be used for the production of haploid amphibian larvae were reviewed a few years ago. Since the mature gametes are haploid, all that is needed is to preserve this condition in the egg as it begins its development. This may be accomplished basically by four routes (cf. Fankhauser, 1937a, frontispiece):

(1) by stimulating the haploid, unfertilized eggs to development by artificial means, e. g., by pricking with a needle—*parthenogenesis*;

(2) by fertilizing normal eggs with spermatozoa that had been treated previously with an agent which incapacitates the sperm chromosomes without suppressing sperm motility (radiations, chemicals such as trypaflavine, sodium fluoride)—*gynogenesis*;

(3) by fertilizing eggs the chromosomes of which have been damaged previously by radiation or removed by operative techniques, with normal spermatozoa, so that development takes place with the sperm nucleus alone—*androgenesis*;

(4) by dividing the egg shortly after fertilization in such a way that one fragment contains the egg nucleus, the other the sperm nucleus; the former fragment, as a rule, does not make more than an attempt at development, since in the majority of cases the isolated egg nucleus divides abnormally or not at all—"*gyno-merogony*" (Fankhauser, 1937b); the fragment with the sperm nucleus usually divides and may give rise to a haploid larva—"*andro-merogony*."

More recently haploid larvae have been obtained accidentally by treating fertilized eggs with cold (Fankhauser and Griffiths, 1939, Griffiths, 1941, *Triturus viridescens*; Fankhauser, Crotta, and Perrot, 1942, *Triturus pyrrhogaster*; Costello, 1942, *Triturus similans*; Fankhauser and Humphrey, 1942, axolotl; see Table 5); with heat (*Triturus pyrrhogaster*, unpublished, see Table 7); or with hydrostatic pressure (Rugh and Marsland, 1943, *Rana pipiens*). In such cases it is usually not known whether development took place by androgenesis or gynogenesis. A single haploid larva of the axolotl, out of a total of 26 haploids found among 1017 larvae developed from refrigerated eggs has given evidence of its origin. Since it was derived from a mating between a recessive white female and a heterozygous dark male and itsel showed dark pigmentation, it must have developed androgenetically (Humphrey and Fankhauser, unpublished).

There is indirect evidence that gynogenesis may also take place in cold-treated amphibian eggs. Eggs of toads (*Bufo*) and tree frogs (*Hyla*) fertilized by spermatozoa of frogs (*Rana*) do not develop beyond the blastula stage when raised at room temperature. However, if they are cooled to 0°C for 5 to 20 hours shortly after insemination, some of them pass through gastrulation and develop into larvae most of which are haploid (Rostand, 1933, 1934, 1936). The low temperature apparently prevents the fusion of the egg and sperm nuclei, with the result that the egg nucleus alone takes part in development. It is possible that a similar inhibition of the sperm nucleus by the cold treatment also takes place in some eggs that had been fertilized by sperms of the same species.

Possibility of parthenogenetic development in salamander eggs. The eggs of frogs and salamanders, although they are very similar in their general appearance, differ markedly in some phases of their earliest development. Fertilization of frog's eggs is strictly monospermic under normal conditions, and the entrance of a single additional spermatozoon makes normal development impossible. In salamanders, on the other hand, the majority of the eggs are polyspermic to a varying degree, but the accessory sperms are prevented by some inhibitory mechanism from dividing and thus disturbing the normal progress of cleavage. The two types of eggs also differ in their reaction to agents inducing parthenogenesis. Puncture with a fine needle is effective with the frog's egg, but completely ineffective with that of *Triton taeniatus* (Bataillon and Tchou-Su, 1929, p. 806). Negative results with eggs of other species of salamanders are not conclusive because of the small number of experiments performed. However, salamander eggs may respond better to other treatments inducing parthenogenesis. Böök (1941) mentions the fact that treatment at +1.4° to +2.8°C for four to seven hours induced cleavage in three out of four unfertilized eggs of *Triton taeniatus*, although their development did not proceed beyond the gastrula stage. Bataillon (1904) had been able to obtain development up to the gastrula stage in eggs of *Rana fusca* exposed first for half an hour to 35°C, then raised at 15–16°C in 6 per cent cane sugar. Recent experiments with unfertilized eggs of *Triturus viridescens* (Wagner, 1944) showed that exposure to 36°C for 25 to 33 minutes, whether or not it was followed by a short cold treatment, induced development to blastula or gastrula stages without treatment with cane sugar solution in a considerable number of cases. One of these eggs gave rise to an embryo the chromosome number of which has not been checked as yet. In other eggs exposed to the same treatment, incomplete furrows were formed. Exposure to cold alone (+2°C) for several hours produced attempts at cleavage in a varying proportion of eggs, but no blastulae.

The problem of the origin of diploid parthenogenetic or gynogenetic larvae. The great majority of parthenogenetic frog tadpoles are dwarfed, weak, and unviable. However, ever since the beginning of the experiments of traumatic parthenogenesis occasional tadpoles have appeared which were normal, vigorous, and on examination of their cells were found to be diploid. The possible origin of these diploid individuals has been discussed many times and at great length. The most recent reviews may be found in Rostand (1938), Kawamura (1939a), Parmenter (1940), and Tyler (1941). This problem is of interest here because it is closely connected with that of the origin of triploid and other polyploid individuals from fertilized eggs. The various possibilities may be classified into three groups:

(1) doubling of the chromosome number by an initial monastral, anastral, or abnormal amphiastral mitosis of the haploid egg nucleus, followed by normal mitosis. Such a process should produce delay in the appearance of the first cleavage detectable in the living egg;

(2) complete suppression of the first or second maturation division, or retention of the haploid set normally eliminated in the second polar body, indicated in the living egg by the failure of the first or second polar body to appear;

(3) production of a diploid egg from a tetraploid oocyte through normal meiosis, a process to which no clue could be found in the appearance of the living egg.

The majority of diploid tadpoles whose cleavage histories are known originated from eggs showing a delay in the appearance of the first cleavage furrow corresponding to one or two nuclear divisions. This suggests, although it does not prove, an origin of the diploid chromosome number according to one of the routes mentioned under (1). The cases with undelayed cleavage may have originated by any of the accidents listed under (2) and (3). Bataillon and Tchou-Su (1929) pointed out that diploid eggs might occur spontaneously with sufficient frequency to account for the origin of all diploid parthenogenetic tadpoles.

That suppression or revocation of the second maturation division, which has reached the metaphase stage at the time of fertilization or treatment, may play a rôle is indicated by the observations of Rostand (1934, 1938) on cross-fertilized eggs of toads and frogs. Refrigeration of the freshly fertilized eggs not only induced gynogenesis, as mentioned above, but also a great rise in the proportion of viable diploid tadpoles that appeared among the expected haploid ones. Presumably the cold treatment which incapacitated the foreign sperms also caused the retention of the second polar body in some of the eggs.

(b) Triploidy

Cold treatment. The first method for the induction of triploidy in normally fertilized amphibian eggs was suggested by Rostand's experiments on cross-fertilized eggs of toads and frogs discussed earlier. If prolonged refrigeration of these eggs fairly often produces diploid, gynogenetic tadpoles through suppression of the second maturation division, similar treatment of normally fertilized eggs should lead to the production of triploid embryos.

The first experiments were carried out by Griffiths in 1938 with eggs of *Triturus viridescens* and demonstrated at once the effectiveness of this simple method. If the eggs were transferred to a constant temperature bath kept at from 0° to +3°C within a few minutes after fertilization and treated for from five to twenty-four hours, the great majority of the larvae developing from the treated eggs were found to be triploid (Fankhauser and Griffiths, 1939; Griffiths, 1941). If, on the other hand, refrigeration was delayed for thirty minutes, it was no longer effective. By that time the second maturation division, which in *Triturus*, as in other amphibian eggs, is arrested in metaphase until fertilization takes place, has progressed to late anaphase (Fankhauser and Moore, 1941a) and can no longer be stopped by the low temperature.

Since 1939 the refrigeration method has been applied to many more eggs of *Triturus viridescens*, as well as to eggs of four other species of salamanders (Table 5). The productiveness of this treatment is remarkable, particularly in *Triturus viridescens*, where 78 per cent of all the larvae so far obtained from refrigerated eggs were found to be triploid. The low number of triploids obtained by Costello with eggs of *Triturus similans* may be explained by his statement that the treatment began at various times after laying; in many cases it was probably too late to prevent the normal formation of the second polar body. In Böök's experiments with eggs of *Triton taeniatus*, the relative inefficiency of the treatment may have been caused by the fact that after the exposure to cold, he allowed the temperature to rise slowly from about 1.4° to 21°C. In our laboratory the eggs are transferred abruptly from room temperature to the cold bath and back, since the investigators who have used extreme temperatures for the induction of polyploidy in plants seem to agree that the rapid change in temperature, the shock, is more important in producing the desired effect on mitosis than the actual temperature employed. Special experiments to test this point have not yet been carried out.

On the other hand, eggs of different species also differ in their reaction to the same cold-treatment, as a comparison of the results obtained with *Triturus viridescens*, *T. pyrrhogaster*, and the axolotl indicates. Moreover, although eggs of the same species are given what may be considered the optimum treatment, different series of experiments will give different percentages of triploid larvae, largely because the eggs deposited by different females differ in their response to cold. Those of a considerable number of females of *Triturus viridescens* have yielded 100 per cent triploids, while those of others produced less than 33 per cent. This difference cannot be explained by the fact that females from different localities were used in the experiments, as has been suggested before (Fankhauser, 1942, p. 28); but the possibility that the eggs react differently to the same treatment in the winter and spring has not been ruled out completely so far.

Differences between individual females tested at the same time are very pronounced in the axolotl, where the eggs of certain females were found to be completely refractory to refrigeration and produced 100 per cent diploid larvae.

It would be interesting to know the complete range of low temperatures that are capable of inducing triploidy. The experiments carried out so far do not demonstrate a simple relation between degree of temperature and percentage of triploids produced (Table 6). As a whole, temperatures above 4°C are clearly less effective, but some triploid larvae have been obtained with treatments at a temperature slightly over 6°C.

The effect of variations in the duration of the

TABLE 5

Summary of results of refrigeration experiments with eggs of several species of salamanders

Temperature: 0° to 4.35°C.
Duration of treatment: usually from 5 to 24 hours (cf. Table 6).

SPECIES	NUMBER OF EGGS TREATED	NUMBER OF LARVAE OBTAINED	CHROMOSOME NUMBER			
			triploid	diploid	haploid	others
Triturus viridescens (results of all experiments performed from 1938 to 1944)	509	264	202 (78%)	50	4	7 haploid/diploid mosaics 1 haploid/triploid
Triturus pyrrhogaster (Fankhauser, Crotta, and Perrot, 1942)	117	29	13 (44.8%)	11	4	1 hyperdiploid (2N + 3 or 4)
Triturus similans (Costello, 1942)	?	100	13	81	4	2 haploid/diploid mosaics
Triton taeniatus (Böök, 1941, 1944)	129	57	5	50	2[*]	—
Axolotl (Fankhauser and Humphrey, 1942, and current exp.)	?	1017	347 (34%)	633	26	1 tetraploid 3 pentaploid 3 hypodiploids (2N – 3 or 4) 2 haploid/diploid mosaics 1 triploid/pentaploid 1 diploid/pentaploid

[*] Three additional haploids were found among the non-viable embryos.

TABLE 6

Effectiveness of temperatures over 4.35°, and of different durations of treatment at 2°C, in inducing triploidy in eggs of Triturus viridescens

(Fankhauser, 1942, Table V, and current experiments of W. T. Powers)

TEMPERATURE	DURATION OF TREATMENT	NO. OF LARVAE OBTAINED	CHROMOSOME NUMBER		
			triploid	diploid	others
4–5°C	5 to 24 hours	14	1	12	1 haploid/diploid mosaic
5.5°C	5 to 24 hours	14	5	9	
5–6.5°	5 to 24 hours	9		9	
6.38°	5 to 24 hours	26	6	20	
Total: 4°–6.38°	5 to 24 hours	63	12	50	1 haploid/diploid mosaic
2°C	30 to 50 min.	3	3	—	
	1 to 2 hours	3	3	—	
	3 to 4 hours	6	6	—	
	4 to 5 hours	5	5	—	
	5 to 7½ hours	16	16	—	
	16¾ to 21 hours	21	21	—	

treatment has also been studied. From the beginning of the experiments it did not seem to make much difference whether eggs of *Triturus viridescens* were refrigerated for five or for twenty-four hours, while a few shorter treatments produced diploid larvae only. However, current experiments of W. T. Powers have shown that cooling for thirty minutes may be sufficient to interfere with the second maturation division (Table 6).

Cold treatment may also induce haploidy in some cases, as has been discussed before, and, more rarely, other deviations in chromosome number, particularly haploid/diploid mosaics. Aneuploid larvae and higher polyploids appear also, but so rarely that they may well represent spontaneous aberrations which were in no way influenced by the treatment.

The mortality among treated eggs varies with the species and, even under the best circumstances, approaches 50 per cent. These figures are not too reliable, since it is not always possible to recognize those treated eggs that failed to develop because they were unfertilized. In *Triturus viridescens*, where the most extensive observations on the early development of treated eggs are available, mortality is highest during early cleavage. The chromosomal condition of such eggs and of more advanced non-viable embryos has not yet been investigated and may show some interesting abnormalities.

Cytological studies of fertilization and early cleavage in refrigerated eggs begun by E. Rogers were interrupted by the war. They will demonstrate the exact nature of the primary effect of the cold treatment. In the meantime it may also be possible to determine directly by observations on living eggs whether or not the second polar body fails to appear, although the polar bodies are not always easily seen in newt eggs, and very small exovates of the size of polar bodies are not infrequently present.

Heat treatment. High temperatures of 38° to 50°C have been used extensively for the induction of polyploidy in plants, both during the maturation divisions and after pollination, during the early divisions of the zygote, to obtain somatic doubling (cf. Fankhauser, 1942, Table 1). Exposure of freshly laid eggs of *Triturus viridescens* to temperatures varying from 35 to 37°C for from five to over fifty minutes was found to be just as effective in inducing triploidy as prolonged refrigeration (Fankhauser and Watson, 1942). These observations have since been confirmed and extended (Table 7). Variations in the duration of the treatment show that the mortality of the eggs rises rapidly with exposures lasting over thirty minutes (Table 8). The ten-minute treatment has been adopted tentatively as the standard exposure because of the lower rate of mortality compared with longer exposures, and because of the higher proportion of triploids produced as compared with five-minute treatments (Erdman and Thompson, 1943).

TABLE 7

Summary of results of heat experiments with eggs of Triturus viridescens and Triturus pyrrhogaster

TEMPERATURE AND DURATION OF TREATMENT	NO. OF EGGS TREATED	NO. OF LARVAE OBTAINED	CHROMOSOME NUMBER		
			triploid	diploid	others
Triturus viridescens					
35 to 37°C, 5 to over 50 minutes (Fankhauser and Watson, 1942)	104	58	49 (84.5%)	9	—
36°, 5 to 25 minutes (Erdman and Thompson, 1943)	74	55	33	21	1 pentaploid
36–37°, 10 minutes (M Criscitiello, unpublished)	23	8	4	4	—
Total		121	86 (71 %)	34	1
Triturus pyrrhogaster					
36–37°C, 10 minutes (unpublished)	24	7	1	4	2 haploids

A single pentaploid larva has been obtained so far in these experiments. It may well have been of spontaneous origin. However, pentaploid larvae may be expected to appear in such experiments if any of the eggs were tetraploid before meiosis. Untreated, such eggs would produce spontaneous triploids; following experimental suppression of the second maturation division they should give rise to pentaploid embryos.

The mortality among heat-treated eggs reaches its highest value during the blastula stage, rather than during early cleavage as in refrigerated eggs. Cytological study of sectioned material will show whether the two types of treatment actually produce different cytological abnormalities that lead to a standstill of development at two distinct periods.

On return to a normal temperature the arrested cells recover rapidly but frequently show multipolar anaphases; tetraploid cells are rare.

A similar reaction of earlier stages of development to cold is indicated by recent experiments of Böök (1944). Of 64 eggs of *Triton taeniatus* treated more than thirty minutes after fertilization but before the first cleavage, thirteen developed normally to neurulae. Study of sections showed that they were complex chromosome mosaics; this condition is designated by Böök as "multiform aneuploidy" and must have arisen as a consequence of multipolar mitoses. Exposure of neurulae to cold produced arrest of metaphases, followed by the formation of restitution nuclei with an increased number of chromosomes.

TABLE 8

Effectiveness of different durations of heat treatment (35–37°C) in inducing triploidy in eggs of Triturus viridescens

AUTHOR	DURATION	NO OF EGGS TREATED	NO OF LARVAE OBTAINED	CHROMOSOME NUMBER		
				triploid	diploid	others
	minutes					
Fankhauser and Watson, 1942 (table 3)	5–9	7	5	5	—	
	10–19	47	34	29	5	
	20–29	24	12	8	4	
	30–over 50	26	7	7	—	
Erdman and Thompson, 1943	5	18	15	6	8	1 pentaploid
	10	43	33	23	10	
	20	10	6	3	3	
	25	1	1	1	—	

A few experiments with eggs of *Triturus pyrrhogaster* carried out this spring showed that the heat treatment also produced chromosomal deviations, including haploidy, in this species; the high rate of mortality among treated eggs is not necessarily an indication of a greater susceptibility of *T. pyrrhogaster* eggs to heat, since it was also unusually high among the untreated controls.

(c) Higher degrees of polyploidy

If cold or heat, when applied during the second maturation division, induce triploidy, the same treatments given during the first cleavage mitosis should inhibit the separation of the chromosomes at anaphase and produce tetraploid embryos. Barber and Callan (1943) studied the effects of cold on mitosis in the tailfin of newt larvae and in spermatogonia of adults and found that the spindle is abnormally developed or completely suppressed.

Preliminary experiments with heat treatments of eggs of *Triturus viridescens* at various times between fertilization and the beginning of the first cleavage produced negative results. This may be explained largely by the fact that it is difficult to time the treatment properly, since the interval between insemination and beginning of anaphase, as determined from sections through preserved eggs, varies considerably between individual eggs kept at the same constant temperature. It is relatively easy to suppress the first cell division by a 20- or 30-minute treatment of the eggs at 36°C, 4 to 5 hours after insemination at 20°. However, at the proper time of the second cleavage such eggs divide at once into four cells showing that the first division of the nucleus had not been suppressed. This can be demonstrated later by the chromosome counts in the resulting larvae, which are always diploid.

Theoretically, doubling of the chromosome number should also be obtainable by appropriate treatments with colchicine solutions. Keppel and Dawson (1939) showed that solutions of sufficient strength to retard or arrest mitosis in eggs of *Rana pipiens* also cause serious abnormalities in development, which does not proceed beyond the neurula stage. Sections of young abnormal embryos show groups of larger, presumably tetraploid, cells, as well as various irregularities of mitosis. Unpublished experiments of Rita C. Watson with eggs of *Triturus viridescens* demonstrated that these react in a similar way. Treatments with weaker solutions (1:5000 or less) had no effect and produced diploid larvae; with stronger solutions (1:1000) abnormal, inviable embryos resulted. In spite of these discouraging reports, more extensive experiments with colchicine and other mitotic "poisons" might still produce the desired results.

The effects of very strong (1%) colchicine solutions on mitosis in the tailfin of newt larvae were investigated by Barber and Callan (1943). Mitosis is arrested at metaphase, and the chromosomes assume various abnormal arrangements. A single, tetraploid resting nucleus may be produced, but recovery of the cells is much slower than after cold treatment because of the slow elimination of the poison, and the larvae rarely survive. In the survivors cell divisions are rare; a single tetraploid cell was seen five days after the end of the treatment.

(d) Experimental "allo-polyploidy" in *Triturus*

Experiments combining hybridization with induction of triploidy by subsequent cold treatment have been reported briefly by Costello (1942). Eggs of *Triturus rivularis*, fertilized by spermatozoa of *T. torosus* and cold treated should produce triploid embryos with two sets of *rivularis* and one set of *torosus* chromosomes. Costello merely states that "no larvae with accentuated maternal characteristics were obtained." Experiments of this type involving various combinations of species should produce interesting results, particularly if it should be possible to induce a doubling of the chromosome number in the zygote and to obtain tetraploid species hybrids.

(e) Polyploid larvae obtained as by-products in other experiments with amphibian eggs

Both Parmenter and Kawamura reported the occurrence of various heteroploid chromosome types among parthenogenetic larvae of frogs, in addition to the haploid and diploid individuals discussed previously. Parmenter (1933) listed a total of 29 embryos and larvae of *Rana pipiens* and *Rana palustris*, of which 12 were haploid, 10 diploid, 4 haploid/diploid mosaics, one diploid/triploid, one diploid/triploid/tetraploid, and one completely triploid. He suggested that the triploid condition resulted from the combination of a retained second polar body with a diploid group which originated through a doubling of the haploid set of the egg nucleus. In experiments with eggs of *Rana fusca*, Parmenter (1940) found 3 haploids, 4 haploid/diploid, one diploid, and 3 diploid/triploid larvae.

Kawamura (1939a), using eggs of *Rana nigromaculata*, obtained the following impressive series of chromosome types among his 413 parthenogenetic larvae: 202 haploids, 86 diploids, 95 triploids, 4 tetraploids, 12 hexaploids, 1 hyperdiploid (2N + 3), and several mosaics (8 haploid/diploids, 3 haploid /triploids, 1 haploid /pentaploid, and 1 triploid/hexaploid). Kawamura discusses in detail the possible modes of origin of the various types. The high frequency of triploids remains unexplained beyond the suggestion that they may have developed from eggs in which (1) the first polar body was retained, (2) two separate second maturation spindles were formed, of which (3) one only was located at the egg surface and produced a second polar body. This would leave three haploid sets of chromosomes in the egg. Such an origin of triploidy was actually described by Hiraiwa and Kawamura (1936) in parthenogenetic eggs of the worm, *Urechis*.

In experiments on androgenesis with eggs of *Triturus pyrrhogaster* Kaylor (1940a) obtained two triploid larvae. The available evidence does not demonstrate beyond doubt that these actually developed androgenetically, i. e., with three paternal chromosome sets, rather than from eggs in which the operative removal of the maternal chromosomes had not been successful.

(f) Experimental heteroploidy in other animals

Experimental induction of heteroploidy has been attempted with relatively few species of animals other than amphibians. The most extensive and successful experiments are those with eggs of the silkmoth, *Bombyx*. Many of the other investigations are incomplete or preliminary in nature. A brief review of the methods used and of the general results obtained follows.

Cold. The brine shrimp, *Artemia salina*, occurs in bisexual and parthenogenetic races. Among the latter, diploid, tetraploid, and octoploid lines are found in different localities; eggs developing parthenogenetically give off a single polar body and retain the chromosome complement of the mother. Refrigeration of parthenogenetic eggs of a diploid race during the single maturation division prevented in some cases the formation of the polar body, so that tetraploid animals may be obtained by this method (Gross, 1932, 1935).

The experiments of Pincus and Shapiro (1939) on the effects of cold on unfertilized rabbit eggs should also be mentioned in this connection. A treatment at +6°C for 10 to 30 minutes may activate eggs in vitro or in the Fallopian tubes. One living young, a female, was obtained from experiments with sixteen rabbits in which probably over 200 eggs had come under the influence of the low temperature. The single female produced apparently was normal and therefore diploid, as might be expected if the cold in this case not only activated the egg but also suppressed the second maturation division.

Heat. Short heat treatments of eggs of the silkmoth (Hasimoto, 1933; Astaurov, 1940) have a double effect: they induce parthenogenesis as well as retention of the diploid chromosome number, since a single, equational maturation division takes place. Furthermore, in over 25 per cent of the heat-treated eggs, there is a tendency for the diploid cleavage nuclei to fuse after the first or a later cleavage mitosis, producing tetraploid or partly tetraploid females. Tetraploid eggs of such females may again be heat-activated and thus give rise to another generation of tetraploid females.

Colchicine. The attempts to induce polyploidy in eggs of various species of animals with colchicine solutions have been rather disappointing so far. The best results were obtained with eggs of the silkmoth which were treated within 2½ hours after laying with 0.05 to 0.4 per cent colchicine and produced "many polyploid individuals" (Hirobe, 1939). The ovaries of the polyploid females, however, were found to contain both polyploid (presumably tetraploid) and diploid cells.

Treatment of females of the wasp, *Habrobracon*, with 0.05 per cent colchicine induced the formation of many tetraploid oogonia in the ovaries. Some of the eggs examined after laying also contained the tetraploid chromosome number (Inaba, 1939, 1940).

Pincus and Waddington (1939) also observed tetraploidy in a number of rabbit eggs after treatments with various mitosis-inhibiting agents, including colchicine and heat; these eggs, however, usually failed to cleave during 24 hours of culture.

Extensive cytological observations on eggs of the fresh-water annelid, *Tubifex*, treated with colchicine showed that the maturation divisions are not inhibited even by strong solutions (1:500). There seems to exist a particularly sensitive period during the interphase following the first cleavage mitosis when the same and lower concentrations cause a complete disappearance of the mitotic apparatus and a dissolution of the nuclei. Concentrations of 1:10,000 to 1:20,000 induce atypical cleavage; with 1:30,000, development is normal. Although mitotic figures with an increased number of chromosomes have been observed in abnormally cleaving eggs, there is no direct proof that these cells are polyploid. The normally developing eggs apparently are all diploid (Lehmann and Woker, 1940; Woker, 1943, 1944).

Treatment of larvae of *Drosophila* produces polyploid areas in brain tissue (Braungart and Ott, 1942), and injection of 0.05 cc. of a 0.05 per cent solution into the body cavity of male grasshoppers may suppress the division of spermatogonia and spermatocytes; the latter may differentiate directly into polyploid spermatids and transform into giant sperm cells with one or more tail filaments (Dooley, 1941).

As a whole the observations seem to show that eggs during early cleavage are so injured by colchicine solutions in concentrations sufficient to affect mitosis that normal development does not take place. Further investigations on the production of diploid or polyploid eggs or spermatozoa by treatment of immature or mature individuals appear to be more promising.

Centrifuging. When eggs of the silkmoth are centrifuged for ten minutes, at 3500 revolutions per minute, from one to three hours after laying (i. e., during the maturation divisions), a considerable proportion of the resulting caterpillars are polyploid. Among 17,193 caterpillars Kawaguchi (1936) found over 13 per cent triploids, over 2 per cent tetraploids, and a single hexaploid individual. More hexaploid caterpillars were obtained by treating eggs deposited by tetraploid mothers.

Hybridization. The earliest experiments which produced polyploid animals were those of Standfuss, Federley, Harrison, and Meisenheimer (bibliography in Goldschmidt, 1931; and Cockayne, 1938), in which F1 males from crosses between several species of moths were mated with females of one of the parent species. Because of the general failure of pairing between the two chromosome sets in the spermatocytes of the F1 males, diploid or nearly diploid spermatozoa are produced which, in fertilizing haploid eggs, give rise to triploid or sub-triploid individuals.

4. Primary effects of changes in number of chromosome sets: changes in nuclear and cell size

The immediate effect produced by a change in chromosome number is a corresponding change in the size of the nuclei and the cells. Because of the constancy of this relationship the alteration in nuclear and cell size can in turn be used as a valuable criterion for the identification of heteroploid individuals (cf. Figs. 1 and 4; Table 2). The measurements on nuclei of heteroploid salamander larvae were made largely for diagnostic purposes and not for an accurate determination of the amount of increase in nuclear volume caused by the addition of each successive chromosome set. The great range of variability between individual nuclei, and between samples of nuclei from different individuals having the same number of chromosomes, would call for very large series of measurements. Also, no attempt has been made so far to determine accurately the changes in the size of the cells, since their boundaries are usually not clearly marked. Although it is evident that the cell size increases with the nuclear size, it is not possible to state whether or not the nucleoplasmic ratio remains constant at all levels of polyploidy.

More or less accurate determinations of the volume of the nuclei in triploid, diploid, and haploid amphibian larvae have been made by several investigators. In these calculations, the nuclei are usually treated as spherical or nearly spherical, and the ratio of the volumes is obtained by comparing the cubes of the radii. The diploid/triploid ratio was generally found to be close to 1:1.5 in nervous tissue, cartilage, and muscle cells (G. and P. Hertwig, 1920, *Rana esculenta*; Kawamura, 1939a, *Rana nigromaculata*). Böök (1944) gives the same ratio for spermatocytes in adult *Triton taeniatus*, while for nerve, cartilage, and muscle cells of larvae he finds a ratio varying between 1:1.63 and 1:1.74.

The haploid/diploid ratio is usually near the expected 0.5:1.0 value (O., G., P. Hertwig, 1913 to 1920). In cartilage nuclei of *Triton taeniatus*, G. Hertwig (1927) found a ratio of 0.31:1.00, but a higher value of 0.60:1.00 is given by both O. Hertwig (1913) and Böök (1941) for nuclei of the medulla in larvae of the same species.

Comparison with invertebrates

In spontaneous and experimentally induced polyploid invertebrates the nuclei are generally larger (*Drosophila, Bombyx*). In the latter, eggs of tetraploid females have roughly one and one-half times the volume of those of diploid individuals (Astaurov, 1940) Kawaguchi (1936) mentions that the eggs of hexaploid females are still larger and gives the following ratios for cross-sectional areas of nuclei of primary spermatocytes: diploid/triploid/tetraploid = 1.0/1.4/1.9. This shows that the volumes of the nuclei increase more than in direct proportion to the chromosome number, since with direct proportionality of the volumes the areas of the cross sections should be as 1.00/1.31/1.58, if the nuclei are spheres. The cells of triploid silk glands are also larger than expected.

In those species of invertebrates in which permanently polyploid, parthenogenetic races occur, the nuclei and cells are also generally larger than in corresponding tissues of diploid animals, e. g., in the triploid race of the crustacean, *Trichoniscus* (Vandel, 1928), and in the tetraploid and octoploid races of the brine shrimp, *Artemia salina* (Artom, 1925). In *Artemia*, the tetraploid/diploid ratio varies between different tissues (Artom, 1923). Recently Barigozzi (1941) described very large differences between individual females of an octoploid race in the average size of the nuclei of the gut epithelium. Major deviations from the average tend to be the same in mother and offspring, indicating the influence of genetic factors; however, it is certain that even the extreme deviations are not connected with any change in chromosome number. It is not known whether changes in the size of the chromosomes or differences in specific genes affecting nuclear and cell size are involved. In the bagworm moth, *Solenobia*, Seiler (1936) found the unusual situation that eggs of tetraploid females are of the same size as those of diploid females but are twice as numerous. The somatic cells are apparently larger in the tetraploid individuals, as is shown by their larger body size.

The relation of cell size to chromosome number is of particular interest in the Hymenoptera, where the males are normally haploid and parthenogenetic, while the females are diploid and develop from fertilized eggs. Male bees did not show consistently smaller nuclei in the many tissues studied by Oehninger (1913). In the parasitic wasp, *Habrobracon*, Speicher (1935) found an increase of about 5 to 16 per cent in the average area of the wing cells of diploid females as compared with haploid males; however, in diploid, biparental males, which occur occasionally, the wing cells were about 28 per cent larger than in diploid females, and in triploid females the increase over diploid females was about 86 per cent. The latter figure may not be reliable, since the triploid females differed from the diploid by a gene affecting the structure of the wings. Similar observations have been made on the size of the facets of the eye, which are produced individually through the secretory activity of two cells (Speicher and Speicher, 1940; Risman, 1942).

Altogether these observations indicate that in the normal, haploid males the size of the cells has been readjusted to nearly normal dimensions through some process of regulation, possibly through a slow selection of genes increasing the cell size. In exceptional diploid males and in their triploid daughters, on the other hand, no regulatory mechanism of this type could be developed, since they occur sporadically and are not exposed continually to the action of selection.

It should not be forgotten, furthermore, that in the Hymenoptera the study of the cell size/chromosome number relationship is complicated by the fact that certain tissues of normal haploid males and diploid females regularly become polyploid to a variable degree during development, as is the case in many other insects (Dodds, 1938, on gallwasps).

Comparison with plants

Studies on the relation of cell size to chromosome number in plants have demonstrated a striking difference between the experimentally induced and occasional, spontaneous polyploids in normally diploid species, on the one hand, and the naturally occurring polyploid races and species on the other. In the latter, there is no consistent relation between chromosome number and cell size (cf. Darlington, 1937). Of 48 naturally tetraploid races investigated, only 14 possessed larger cells (Müntzing, 1936). In induced polyploids there is a close proportionality between cell size and chromosome number. In *Nicotiana*, for instance, the cells increase throughout the plant with the addition of each chromosome set, from the haploid to the octoploid condition (H. H. Smith, 1943). As in animals, the polyploid/diploid ratio may vary between different tissues. In the periwinkle, *Vinca rosea*, the guard cells of the stomata are much larger in tetraploid leaves and can be used to identify polyploid individuals, as in other plants. The ordinary epidermal cells, however, are of about the same size as in diploid leaves (Cross and Johnson, 1941). In maize, the nuclei and cells of the shoot apex are almost exactly twice as large in tetraploid seedlings as in diploid ones. In the mature leaf, the average size of the tetraploid cells is only 1.6 times the diploid size; furthermore, the variability in different tissues and in the same tissue in different regions is very great (Randolph, Abbe, and Einset, 1944).

The nucleoplasmic ratio (or cytonuclear ratio, cf. Sinnott and Trombetta, 1936; Trombetta, 1942) may not remain constant with higher degrees of polyploidy. In *Crepis capillaris* the ratio of the volumes of the nuclei in meristem cells of the root of a diploid, a triploid, and a pentaploid plant was 1:1.9:4.1, the ratio of the cell volumes 1:1.3;2.5 (Navashin, 1925). Endosperm cells of tetraploid maize show an opposite trend. In diploid plants these cells are regularly triploid, since their nuclei are derived from a process of fusion between three haploid nuclei at the time of fertilization; in tetraploid plants, the endosperm is therefore hexaploid. While their cell volume is 3.5 times the normal, the volume of their nuclei has increased only 2.5 times (Randolph and Hand, 1938, 1940).

The whole problem of the relation of cell size to polyploidy offers special aspects in plants because of the secondary enlargement or expansion of the cells connected with extensive vacuolization. In early fruit primordia of cucurbits the cells are twice as large in tetraploid plants as in the diploid; after cell divisions cease, however, the diploid cells expand more and, at maturity, reach nearly the same size as the tetraploid (Sinnott and Franklin, 1943).

Significant additions to the study of the factors affecting cell size have been made by investigations on mosses, which are normally haploid (cf. Wettstein, 1927). Measurements have shown the existence of specific differences in the increase of cell volume following experimental chromosome doubling. The haploid/diploid ratio may vary from 1:1.45 to 1:3.94 in different species. Recently, Barthelmess (1941) studied nine races of *Physcomitrium piriforme* which differ considerably in the size and shape of the cells in their normal, haploid condition. When diploidy is induced experimentally, the cell volume increases in some races from 1 to 1.64, in other races it actually decreases from 1 to 0.9. Of the greatest theoretical importance are Wettstein's (1937) observations on an experimentally induced diploid clone of *Bryum caespiticium* in which the cell size at first was 37,800 cubic micra, as compared with 16,900 cubic micra in the original haploid plant. In the course of eleven years, however, the cell size was reduced slowly, until it reached the value of 18,600 cubic micra. In a naturally occurring diploid clone of the same species, the cell size was found to be 21,900 cubic micra.

Changes in the shape of cells

Changes in chromosome number may alter different dimensions of the cells to a different degree and thus produce a change in their shape. In tetraploid plants of *Vinca rosea* the cells of the apical meristem are broader but not higher; the lateral dimensions are increased by one-half to two-thirds, while the vertical dimensions may be slightly reduced (Cross and Johnson, 1941). The nine races of the moss *Physcomitrium* studied by Barthelmess (1941) varied not only in cell size but also in cell shape. Chromosome doubling produced a broadening of the cell in races with narrow cells in the normal, haploid condition; in races with short haploid cells, diploidy caused the cells to become longer and narrower.

Changes in the shape of the nuclei may also be associated with heteroploidy in salamander larvae. The nuclei of haploid erythrocytes are relatively shorter and more rounded than those of diploid cells, and the nuclei of haploid connective tissue cells also tend to be less irregular in shape. A decrease in the length/breadth index of the nuclei of haploid erythrocytes and kidney cells has also been described by Böök (1941). This might be a simple consequence of the different surface properties of the smaller haploid nuclei. Changes in the shape of cells are conspicuous in organs where they are arranged in thin layers, as in the epidermis or in the kidney tubules. This is a point of considerable theoretical importance, to be discussed in a later section.

5. *Secondary effects of changes in chromosome number*

Most of the macroscopic effects of heteroploidy, both morphological and physiological, may be termed secondary, since they appear to be consequences of the changes in nuclear and cell size which are the primary results of alterations in chromosome number. It must be emphasized, however, that frequently it will not be easy to determine whether the ultimate cause of a visible effect is to be found solely in the change in the total mass of chromosome material affecting the size of the nuclei and cells, or, partly or entirely, in the change in the dosage of genes, which may influence the expression of certain individual genes while that of others remains the same. The latter case would represent a second type of primary effect of heteroploidy (see p. 121).

On the other hand, it might be possible to classify some of the effects described in the following pages as still more remote links in the chain of reactions set up by the initial change in chromosome number, i. e., as direct or even indirect consequences of some secondary effect. Until we know a great deal more about the causation of some of the expressions of heteroploidy in amphibian development it will suffice to keep these various possibilities of interpretation in mind for a future reconsideration of the facts.

In view of the close interrelations between all the processes of development, it may be misleading to treat them separately in the discussion. For the sake of clarity, however, it would seem advantageous to group the facts under the following headings which will help us to focus our attention consecutively on the various problems that are involved.

(a) Body size, organ size, and their relation to cell size and cell number

Haploidy. All investigators agree that haploid amphibian larvae are smaller than normal to a varying degree (Fig. 7). The earliest detailed observations by O. Hertwig on *Triton taeniatus* indicated a reduction in body length and in the size of many organs to three-fourths or two-thirds of the normal measurements. Recently, Böök (1941) described a similar reduction in the size of a larva of the same species, and estimated that the volume of the central nervous system was about 61 per cent of the normal. In anurans, G. Hertwig (1913) found twice the normal cell number in haploid gastrulae but a reduction in later stages of development, so that the individual organs were only half normal size, with the exception of the ear vesicles, which were as large as in diploid larvae. Porter (1939) mentions that in haploid tadpoles of *Rana* *pipiens* the notochord has the same cross sectional area as in the diploid while the other organs are clearly reduced. Such exceptional reactions of single organs have considerable interest for the study of the factors controlling growth and organ size and should be investigated more closely.

The relation of size and cell number was studied in lenses developed from haploid epidermis which had been transplanted to the eye region of diploid embryos (Rotman '40). At the time of separation from the epidermis, the lens had the same size as the diploid on the unoperated side and contained about 69 per cent more cells per unit volume. A similar relation was found in a completely haploid control embryo; this would indicate that an adjustment in cell number compensating for the decrease in cell size may take place very early in development of an organ, although in the case of the lens this regulation may be largely dependent on the size of the optic cup inducing its formation in the overlying epidermis.

The fact that the haploid larvae which appeared spontaneously in several species of salamanders in our own laboratory were also more or less dwarfed demonstrates clearly that the various treatments which are used to induce haploidy experimentally are not responsible for this effect (Fig. 7: 1–2). The size of individual haploid larvae varies considerably, however, and in at least one case, a larva developed from a refrigerated egg of *Triturus pyrrhogaster*, was almost normal (Fig. 7: 4).

A detailed investigation was made of the microscopical anatomy of the oldest haploid salamander obtained so far which died at the conclusion of metamorphosis (Baltzer, 1922; Fankhauser, 1938a). The animal was dwarfed (cf. Fankhauser, 1937a, Fig. 6) but more than half normal size. Correspondingly, most of the organs were larger than half size, with more numerous cells than the diploid organs, with the exception of the cartilages of the larynx, which showed the same cell number in cross section and were almost exactly half size. On the other hand, some glands attained normal size, either through enlargement of the individual structural units, such as the tubules of the lacrymal glands, or through an increase in the number of the units which remained small themselves, as in the case of the follicles of the thyroid.

It must be mentioned that this haploid developed from an egg fragment, which included considerably more than half of the mass of the egg. The initial mass of cytoplasm and yolk has been shown to be of little importance, however, since diploid larvae from egg fragments or isolated blastomeres of the two-cell stage, although half-size at first, reach approximately normal size at the time of metamorphosis (Spemann and Falkenberg, 1919, *Triton taeniatus*; also unpublished observations on *Triturus viridescens*).

Triploidy. Triploid salamander larvae, as a rule, are not noticeably larger than the diploid. In *Triturus viridescens* the size range of triploids is approximately normal (Fig. 5); a single larva among the many which have been raised to metamorphosis so far was considerably larger (Fankhauser, 1938c). The influence of differences in the amount and kind of food given to the larvae can be eliminated by maximal feeding with *Daphnia*, which may be accomplished by having *Daphnia* present in the culture dishes at all times, or, still better, by raising the larvae in large *Daphnia* cultures. The latter method produced particularly vigorous animals, but again, diploid and triploid larvae responded in the same way. In *Triturus pyrrhogaster*, observations on a smaller number of animals showed that maximal feeding may bring out a slightly greater response in triploids (Fankhauser, Crotta, and Perrot, 1942). Triploid *Eurycea* larvae may or may not become slightly larger than the controls; in some cases they are even smaller (Fankhauser, 1939; Michalski, 1942). In axolotls, which can be easily raised to sexual maturity in the laboratory, it will be possible to settle the question of the final size reached by adult triploids. So far, observations on numerous larvae have shown that in some spawnings the triploids are uniformly large and vigorous, while in others they are lagging behind the controls.

In triploid *Triturus viridescens* the normal size of the organs at the time of metamorphosis is caused by a decrease in the number of cells that neutralizes the increase in cell size (Fankhauser, 1941a); the notochord alone may be an exception, since it appears larger in cross-section. The gonads present a special case, since their development is influenced by the disturbance of the sex chromosome mechanism and will be discussed later.

In general, the observations on triploid amphibian larvae made in other laboratories are in agreement with our findings. Böök (1944) reports that triploid larvae of *Triton taeniatus* are normal in size and have fewer cells in all the organs studied. The only adult triploid salamander found so far was large but within the normal size range of diploid animals (Böök, 1940). On the other hand, Parmenter (1933) noted that a triploid parthenogenetic tadpole of *Rana pipiens* was conspicuously large. The observations of Kawamura (1939a) on numerous triploid parthenogenetic larvae of *Rana nigromaculata* are difficult to evaluate because of the high proportion of abnormal individuals present. His drawings show a similar range of body size in triploid and diploid tadpoles although the former seem to be somewhat smaller on the average.

Higher degrees of polyploidy. Of the few tetraploid larvae seen so far, the first two, found in *Eurycea bislineata*, were slightly smaller than the controls from the beginning of the observations. The single tetraploid larva of *Triturus viridescens* was smaller at hatching but finally reached approximately normal size at metamorphosis, although with considerable delay (Fig. 5: 7).

All of the eight pentaploid larvae of *Triturus viridescens* seen so far were approximately normal in size at the time of hatching (Fig. 6: 1–2; cf. Fankhauser, 1940). The three which were raised to metamorphosis were greatly retarded in development but metamorphosed at about normal size (Fig. 6: 5). This was also true of a single pentaploid larva of *Triturus pyrrhogaster* which was discovered last spring (Fig. 6: 6–8). Two pentaploid axolotl larvae likewise remained behind the diploid in size as long as they lived.

Tetraploid and hexaploid individuals were found by Kawamura (1939a) among his parthenogenetic frog tadpoles The size of the young larvae was within the diploid range as far as can be told from the illustrations; none of the animals were raised to a more advanced stage.

Cursory examination of sections through tetraploid and pentaploid salamanders shows at once that throughout the body the larger size of the cells is met by a decrease in cell number. As far as the observations go we may conclude, therefore, that the body size of polyploid amphibian larvae at comparable stages of development is always the same, irrespective of the chromosome number and the cell size, since the latter is compensated by a corresponding reduction in the number of cells. Haploid larvae as a rule are smaller but show at least a partial compensation in cell number (cf. Sharp, 1943, Fig. 157).

Comparison with invertebrates. The classical studies of Boveri (1905) on eggs of sea urchins, which first demonstrated a constant relationship between chromosome number, nuclear and cell size in animals, also showed that the size of the young embryo at the end of cleavage is not affected. A haploid gastrula consists of smaller but more numerous cells, a tetraploid contains larger but fewer cells. At the early pluteus stage haploids are smaller (cf. Hoerstadius and Wolsky, 1936); no information on the later development of polyploid eggs seems to be available.

The relation of chromosome number to adult body size in various species of arthropods was discussed at length in a previous publication (Fankhauser, 1941a, pp. 166–7, Table 2). Gigantism was reported in tetraploid and octoploid brine shrimps, *Artemia*, although various statements indicate that this may not be the general rule in this species. Artom (1927, 1928, 1929) emphasizes the pronounced gigantism of embryonic stages, in which the total cell number seems to be normal, while in the adult tetraploid the "potential" gigantism may be masked by suboptimal environmental conditions. He also stresses the fact that the gigantism may be restricted to organs with constant cell number, as the central nervous system or the eyes; the same ganglion, for instance, is made up of from 115 to 130 cells in both diploid and tetraploid individuals. Octoploid Artemia are hardly larger when they reach sexual maturity, but seem to grow larger with age (Gross, 1932).

In the bagworm moth, *Solenobia*, pupae of the tetraploid race are twice as large as diploid pupae, while triploid pupae are intermediate though very variable (Seiler, 1927, 1936, 1937). Females of the triploid race of the isopod *Trichoniscus* are 4.5 mm. long on the average, diploid females average 3.3 mm. (Vandel, 1927, 1928). In *Drosophila melanogaster*, triploid females are characterized by large, stocky build, large, roughish eyes with large ommatidia, and by coarse bristles (Morgan, Bridges and Sturtevant, 1925). According to Dobzhansky (1941), they differ from the diploid in body proportions rather than in actual size. Triploid females of *Drosophila americana* are somewhat larger and stockier and have roughened eyes (Stalker, 1942).

Triploid and tetraploid silkworms are not larger than the diploid, according to Kawaguchi (1936) and Astaurov (1940), because the cell number is reduced in inverse proportion to the cell size, e. g., from 680 to 443 in triploid silk glands. In this species the reactions to changes in chromosome number thus seem to be identical with those shown by amphibian larvae.

Comparison with plants. From the great mass of available data a few striking illustrations have been selected, from recent publications, to show the general trends. Long established polyploid races or species may or may not show gigantism, depending in many cases on whether or not the size of the individual cells has returned to normal (cf. Darlington, 1937). Spontaneous and induced tetraploids in diploid species are consideraby larger than diploids as a rule, while triploids are intermediate in size (cf. Müntzing, 1936). In *Nicotiana*, for instance, there is a general increase in the size of the plant from the haploid to the tetraploid condition (H. H. Smith, 1943), parallel to the increase in cell size. In corresponding cross sections of diploid, triploid, and tetraploid roots Warmke and Blakeslee (1939) found approximately the same total number of cells and the same number of cell layers (about six) in the cortex.

The increase in plant size may continue with the addition of a fifth and sixth set of chromosomes (e. g., in hexaploid *Cuthbertia*, Giles, 1942). Octoploid plants, however, are smaller than the diploid as a rule in spite of their large cells (*Nicotiana*, Greenleaf, 1938, H. H. Smith, 1943; *Cucumis*, Shifriss, 1942; *Galeopsis*, Müntzing, 1941; maize, Randolph, unpublished, cf. Greenleaf, 1938, p. 458).

The effects of haploidy may also differ in different species. In *Datura stramonium* and *D. Metel*, for instance, haploid plants are less vigorous and dwarfed, as is the general rule in other genera of plants. In *Datura pruinosa* they are nearly normal in size (Satina, Blakeslee and Avery, 1937).

The potential gigantism of polyploid plants may be greatly influenced by both environmental and hereditary factors. Tetraploid individuals of the cucumber, which are more vigorous when grown in the greenhouse, do not show *gigas* characters in the field (Shifriss, 1942). In maize, tetraploid plants in non-inbred strains show normal or increased vigor; in inbred strains they are much shorter and less vigorous than diploids (Randolph, 1942).

Of the greatest interest from our standpoint are recent developmental studies on polyploid plants which have shown that the embryo as a whole, or the rudiments of various organs, may show typical *gigas* characters which are modified or completely lost during later stages of development. According to Fabergé (1936), tetraploid embryos of the tomato are 30 per cent heavier than normal but lose this advantage during the first eleven days after sowing, so that the tetraploid plant may not differ significantly in the total amount of substance produced. In maize, the shoot apex of tetraploid seedlings shows "ideal" *gigas* characters, while the volume of the mature leaf is only 1.6 times the normal, although the total cell number is approximately the same as in a diploid leaf (Randolph, Abbe, and Einset, 1944). In squashes, the young tetraploid ovary is about twice as large as the diploid, but the mature fruit is normal in size because the expansion of the cells following the cessation of cell multiplication is much reduced (Sinnott and Franklin, 1943).

This last observation indicates that in plants, as well as in animals, the quantitative effects of the initial change in cell size may be cancelled completely, although this compensation is achieved here, not through a reciprocal change in cell number, but through a modification of the secondary expansion of the individual cells by vacuolization, a process which is of great importance in plants but absent in most animal tissues.

(b) Rate of development

Haploidy. The development of haploid amphibian embryos is significantly slower than that of the diploid (Fig. 7: 1, 2, 5; cf. the series of photographs in Fankhauser, 1937, Figs. 2 to 4). In most of the haploid eggs or egg fragments of various species of newts, cleavage is slower than in the controls; usually there is a pronounced delay already in the appearance of the first cleavage furrow (O. Hertwig, 1913, Spemann, 1914, Baltzer, 1920, *Triton taeniatus*; Fankhauser, 1925, 1934a–c, Hadorn, 1932, 1934, *Triton palmatus*; Kaylor, 1937, Fankhauser and Moore, 1941a, *Triturus viridescens*; Fankhauser, 1937a, Kaylor, 1940, *Triturus pyrrhogaster*). Böök (1941) alone reported an accelerated rate of cell divisions in a haploid egg of *Triton taeniatus*. In anurans, on the other hand, the cleavage of haploid eggs takes place at the normal rate, while later development, from the gastrula stage on, is retarded (Parmenter, 1933, Porter, 1939, *Rana pipiens*).

It would be important to know whether the rate of growth and the rate of differentiation are affected to different degrees by haploidy. That cell division, the basic process of growth, is slowed down in haploid cells is shown not only by the lower rate of cleavage in haploid eggs of salamanders, but also by the lower rate of regeneration of the tailtip following amputation in the young larva (*Triturus viridescens*, *T. pyrrhogaster*), and by the behavior of haploid limb buds or differentiated limbs when transplanted to diploid embryos or larvae (G. Hertwig, 1927).

The retardation of the process of gastrulation, on the other hand, which in androgenetic eggs of *Triturus viridescens* may begin from six to nine hours later than in controls and take 32 instead of 24 hours (at 21°, Kaylor, 1937), indicates that the morphogenetic movements which are largely associated with changes in the shape and arrangement of cells (Holtfreter, 1943) are also affected. Retardation in the differentiation of various organs is mentioned specifically by P. Hertwig (1916, *Triton vulgaris*), while G. Hertwig (1913, *Bufo vulgaris*) stresses the delayed differentiation of the ear vesicles and liver, and Porter (1939, *Rana pipiens*) notes a similar retardation in the differentiation of the eye and gut.

The single haploid salamander that could be raised beyond the early larval stage showed pronounced retardation in later development, including the onset of metamorphosis (Baltzer, 1922). At the completion of metamorphosis, all the organs seemed to be essentially normal histologically and to have reached the same degree of differentiation as in a diploid animal in a corresponding final stage of transformation (Fankhauser, 1938a).

This problem should be analysed by the culture of haploid tissues in vitro where the detrimental influence of the generally lowered viability of the haploid organism as a whole may be eliminated. Observations on four explants from haploid gastrulae of *Triton alpestris* (Hadorn, 1934, pp. 722–724), which were made to compare their performance with that of tissues of haploid androgenetic hybrids, did not show any striking differences from diploid explants. In this connection recent observations on the growth rate in vitro of excised tomato roots are of interest, as showing that under the favorable conditions of the culture haploid roots may grow as well as diploid (Robbins and Kavanach, 1943). It must be pointed out, however, that haploid individuals of tomatoes and other species of plants may grow surprisingly well when compared with diploids. Lindstrom (1936, p. 208) mentions that both growth and regeneration (from cuttings or from callus) are faster in haploid plants than in diploid, a statement which would hardly seem to apply to plants in general.

Polyploidy. The general rate of development of triploid salamander eggs is entirely normal with regard to both growth and differentiation, as far as can be told from the appearance of the living embryos and larvae. In later stages of development the growth rate may remain the same as in the diploid or may increase slightly (*Triturus viridescens*, *Triturus pyrrhogaster*, *Eurycea bislineata*). Among axolotl larvae, the growth rate is about the same in triploids as in diploids; in one spawning, the triploid larvae seemed to lag in growth (unpublished observations of R. R. Humphrey).

The rate of regeneration of the tail and limbs was carefully studied in triploid and diploid larvae of *Triturus viridescens* at various stages of development, but no significant difference could be detected between the two groups of animals (unpublished experiments of Rita C. Watson). This indicates that the rate of division must be normal or nearly normal in triploid cells.

Triploidy often causes a delay in the onset of metamorphosis (Fig. 5: 5–6). The duration of the larval period varies considerably between diploid individuals within a group of common ancestry, raised at the same time, and still more between different groups derived from different matings. These group differences may be partly hereditary, partly caused by differences in diet, since the groups raised on a pure *Daphnia* diet metamorphosed earlier than those which were fed mostly *Tubifex* or *Enchytraeus* worms.

Metamorphosis is most conveniently timed by using the day of the first molt, since the preceding "premetamorphic" changes, like the reduction of the tailfin and gills and the changes in the pigment pattern, are slow and gradual. Between several groups of diploid animals raised during the past four years the average age at the first molt varied from 77 to 115 days, the mean for all 69 animals being 89.4 days. In the corresponding groups of triploids, including a total of 32 animals, the range was from 84 to 145 days, and the mean 102 days.

The few tetraploid salamander larvae that have come under observation so far all developed considerably more slowly than the diploid. The most complete records available are those for the single tetraploid larva of *Triturus viridescens* which, from an early larval stage on, was several days behind in differentiation and growth. Regeneration of the amputated tailtip also was slower than in the diploid. When the diploid larvae entered metamorphosis at the age of eleven to twelve weeks, the body length of the tetraploid was only about three-fourths of the normal. However, this animal remained in the larval stage several weeks longer, growing steadily to approximately normal size when it molted for the first time at the age of nineteen weeks (Fig. 5: 7).

A total of eight pentaploid larvae of *Triturus viridescens* have come under observation so far. The embryonic and larval development, up to almost complete differentiation of the forelimbs, proceeded at a normal rate in the seven animals for which sufficient records are available. Five larvae were preserved at the time of the first appearance of the hindlimb buds, while the remaining three were raised to metamorphosis. Two of the latter remained behind in differentiation, to varying degrees, during the development of the hindlimbs; one proceeded with differentiation at the normal rate to almost complete formation of the toes. In all three, however, the rate of growth was greatly reduced from the time of the appearance of the hindlimb buds on, though again not uniformly. As in the case of the single tetraploid, the animals remained longer in the larval stage than the controls. Two underwent the first molt about three and five weeks, respectively, later than the average diploid; by this time one had reached a size typical for diploid animals at metamorphosis; the other was still considerably smaller (Fig. 6: 4–5). The third pentaploid belatedly showed the typical changes in pigmentation and reduction of the gills and tailfin but died without having molted, eight weeks after the first molt of the average diploid, still strikingly dwarfed when compared with diploids at this stage of transformation (Fig. 6: 3).

The single pentaploid larva of *Triturus pyrrhogaster* found so far also showed a differential effect of the high chromosome number on the rate of growth and differentiation. The latter was delayed slightly during later stages of the development of the hindlimbs, while the growth rate was greatly reduced (Fig. 6: 6). The larval period was again prolonged, so that the animal metamorphosed at a size approximately typical for the species, almost eight weeks later than the diploid controls (Fig. 6: 7–8).

The various metamorphic changes were normal in the pentaploids, as far as could be determined from their external appearance. This does not preclude the possibility that a close study of the sections may reveal some differences in the histological response of various organs. The appearance of the thyroid will be particularly interesting, although it will not decide the question whether the delay in metamorphosis was caused originally by a slower differentiation of this gland and a delayed release of the secretion, or by a tardy response of the reacting tissues to the thyroid hormone.

The slow growth rate of the pentaploids during later larval development may be caused in part by the generally lower food intake of these animals. There are evidences, however, that this is not the only and perhaps not the most important factor. On the one hand, one pentaploid larva, which during most of the larval period took almost as much food as the controls, remained much behind in growth, although not as much as another pentaploid of exactly the same age which fed less. On the other hand, regeneration of the amputated tailtip in the young larvae which had not yet reached the feeding stage proceeded considerably more slowly in the pentaploids. This fact indicates an inherently lower growth rate of pentaploid tissues, since it is well known that sub-optimal feeding, or even starvation, has little influence on the rate of regeneration in older diploid larvae. Experiments on tail and limb regeneration in older pentaploid animals have not yet been carried out.

Comparison with polyploid invertebrates and plants. The available information on the rate of development of polyploid invertebrates is rather incomplete. In the moth *Solenobia*, tetraploid individuals develop more slowly than diploid, while triploids show an intermediate rate (Seiler, 1927). In triploid and tetraploid silkworms the rate of mitosis is decreased apparently in inverse proportion to the increase in chromosome number and cell size (Astaurov, 1940); in eggs containing diploid as well as tetraploid and octoploid cleavage nuclei, the lower mitotic rate of the polyploid nuclei is obvious (Frolowa, 1940). In the brine shrimp *Artemia*, the rate of division of polyploid nuclei is also lower at later stages of development; however, tetraploid embryos grow more rapidly at first and show a precocious differentiation of the organs, particularly of the optic ganglia and the eyes (Artom, 1927).

The observations on the rate of development of polyploid animals are in general agreement with those on plants. The growth of some triploid plants, e.g., *Crepis*, pine-apple, apple, is slower than that of the diploid (cf. Müntzing, 1936); in others it is more rapid, e. g., *Populus tremula* (Nilsson-Ehle, 1936). In experimentally induced tetraploid plants, the time from planting of the seed to beginning of flowering is increased (Kostoff, 1938). In *Nicotiana Sanderae* and *N. Langsdorffii* maturity is delayed more and more with the addition of each set of chromosomes (H. H. Smith, 1943). Tetraploid plants as a rule are slow growing; in octoploids, the rate of growth is reduced still further, e. g., *Nicotiana* (Greenleaf, 1938). In cultures of excised tomato roots, the tetraploids also show a much reduced growth; the dry weight of the tissue produced during a certain period is only one-third to one-half of that of diploid cultures (Robbins and Kavanach, 1943). In those cases where the rate of cell division was studied directly it was found to be reduced in tetraploids (tomato, Lesley and Lesley, 1930; maize, Randolph, Abbe and Einset, 1944; see also Eigsti, 1942).

The first comparison of the growth hormone content of diploid and related tetraploid plants, at the same stage of development and tested on the same day, has just been published by Gustafson (1944). He found that tetraploids of two varieties of marigolds had 58.1 per cent and 76.3 per cent as much hormone, respectively, as the diploids, and tetraploid cherry tomatoes 56.8 per cent as much as the diploids. The general appearance of the young tetraploid plants gave no indication of the lower hormone content; however, they blossomed considerably later than the diploids.

(c) Physiological effects

Haploidy. All investigators agree that the viability of haploid amphibian embryos and larvae is greatly reduced. The rate of mortality at various stages of embryonic and larval development is high; of the several thousand haploid larvae observed by the Hertwigs over a period of years none developed beyond the first larval period (P. Hertwig, 1923). In spite of numerous attempts to raise haploids, Baltzer's (1922) *Triton taeniatus* remains the only haploid to have reached metamorphosis.

The effects of haploidy are not equally severe in different taxonomic groups of amphibians. P. Hertwig (1923) mentions that haploid newt embryos are more normal than those of toads, and these in turn are less affected than frog embryos. Similar differences seem to exist between species of newts, since haploid larvae of *Triturus pyrrhogaster* are more normal as a whole than those of *Triturus viridescens* (Fankhauser, 1937a; Kaylor, 1940a).

The actual causes of the poor viability of haploid embryos are still not well understood (cf. Fankhauser, 1937a, pp. 12–14). The various hypotheses which have been suggested may be briefly summarized under the following headings:

(1) Delayed, harmful effect of the treatment used to induce haploidy. A latent toxic effect on the egg may be associated with radiation of one of the gametes, or with treatment of the sperm with trypaflavine (Dalcq and Simon, 1931). However, it is unlikely that simple operative techniques like the removal of a small amount of egg material with the second maturation spindle should have a deleterious effect. Furthermore, it should be emphasized here that the haploid embryos which have appeared spontaneously in several species of salamanders are not more normal than those produced experimentally.

(2) Edema. The great majority of haploid amphibian larvae sooner or later develop generalized edema, which may be severe enough to cause their death (Dalcq, 1932). A malfunction of the excretory system is the most widely accepted cause of this condition in haploids, although no concerted effort has been made to rule out other possibilities, such as deficiencies of the circulatory system or, perhaps, a general change in the water relations of haploid cells. An interesting approach to the study of this problem was made by Kaylor (1940b), who united haploid with diploid embryos in parabiosis. One of these pairs survived long enough to show the gradual regression of an early edema in the haploid partner when sufficient connection had been established with the circulation of the diploid. The disappearance of the edema, however, did not improve the further development of the haploid member.

In several experiments haploid newt larvae were obtained which were free from edema (*Triton taeniatus*, G. Hertwig, 1927; *Triturus pyrrhogaster*, Fig. 7: 4). Such larvae develop well until the supply of yolk is exhausted. After this they usually cannot be induced to feed, or, in a few cases, begin to take small *Daphnia* but lose their interest in food again after a short while. In such non-edematous animals the factor limiting their life span may well be their generally low reactivity or, perhaps, some more specific sensory disturbance.

(3) Abnormal utilization of yolk supply. The observations of the rate of utilization of the yolk in various organs of haploid embryos are conflicting and have led to the formulation of two diametrically opposed hypotheses. G. Hertwig (1913) found a lower rate of yolk consumption in haploid embryos of anurans and suggested that these embryos die because the slowly growing haploid cells are unable to take care of the normal yolk supply of the egg. Tchou-Su (1931), on the other hand, claimed that the yolk granules disappear more rapidly from the intestinal and germ cells of haploid toad embryos, which thus actually "die from their excessive oxidations." Since haploid embryos have smaller but more numerous cells, the total surface of the nuclei, i. e., the total zone of interaction between nuclei and cytoplasm, would be greater and the rate of metabolism thus increased. Recently, Porter (1939) again noted that in androgenetic embryos of *Rana pipiens* the yolk granules disappear more slowly from various organs than in the controls.

(4) Expression of recessive lethal factors in haploids. A highly suggestive genetical explanation of the poor viability of haploid amphibian larvae was proposed by Darlington (1937) and others. Recessive lethal factors in single dose appear to be widespread in natural populations. When isolated from the normal dominant allele in haploid embryos, they can produce their effect and kill the embryos at various stages of development. This hypothesis does not explain the normal viability of diploid parthogenetic frogs (Parmenter, 1933) and grasshoppers (King and Slifer, 1934), if their diploid condition was produced by doubling of the haploid chromosome set during the first or a later cleavage mitosis, a process which would result in a completely homozygous condition. In other cases diploidy may be the result of the retention of two sets of maternal chromosomes through suppression of a meiotic division, thus maintaining a considerable degree of heterozygosity and accounting for the normal viability of the diploids.

Other physiological effects have been mentioned occasionally without the claim that they represent the ultimate cause of the low viability of haploids. Both O. Hertwig (1913) and Böök (1941) stress the slow and weak contractions of the heart, a condition which may well be a secondary consequence of the reduced vigor rather than its cause. On the other hand, Bataillon found that parthenogenetic frog embryos are more susceptible to heat than are diploid embryos (cf. Rostand, 1938).

From the foregoing it is obvious that little progress can be expected in the analysis of the effects of haploidy until both the structure and the function of haploid organs are investigated much more thoroughly.

Polyploidy. The viability of triploid salamander larvae is normal, on the whole. In *Triturus viridescens* and *Amblystoma mexicanum*, the two species in which the largest numbers of triploids have been obtained, the rate of mortality is not significantly higher than in the controls. Some triploid larvae of *Triturus viridescens*, *T. pyrrhogaster*, and *Eurycea bislineata* show a slightly higher growth rate when abundant food is offered, as was mentioned earlier. It would be interesting to find out whether this is connected with a greater food intake or with a better utilization of the food during digestion. In later stages of larval development triploids may show a greater tendency to develop ascites, a localized accumulation of fluid in the body cavity as contrasted with the generalized edema of haploids. However, ascites could by no means be regarded as a general symptom of triploidy.

The slight increase in growth rate shown by some triploid larvae that were fed "maximally" suggested special experiments to test the reaction of triploid and diploid larvae to pituitary stimulation (Fankhauser and Watson, 1945). Large larvae of *Triturus viridescens*, two to four weeks before the normal time of metamorphosis (first molt), were implanted with three or four adult pituitaries, at intervals of from eight to ten days. The rather paradoxical effect of this treatment was a great delay and partial inhibition of metamorphosis, as had been found by Herre (1935) and Herre and Rawiel (1939) in similar experiments with larvae of *Triton*. Resorption of the gills and tailfin was slow and incomplete. The animals never showed any tendency to leave the water permanently, although several reached an age of six to eight months, and two lived for two and nearly three years, respectively. The two latter had reached an apparently permanent, partially metamorphosed condition with rudimentary gills, fairly wide tailfin, and a pigment pattern quite distinct from that of normal animals. In the implanted animals the first molt took place six to eight weeks later than in the controls, but molting continued as long as the animals lived, in some cases at short and fairly regular intervals of from two to five days.

Growth continued during the first few months but ceased later, in the two animals which lived beyond the first year. Whether or not the growth was at first accelerated in comparison with unimplanted controls is difficult to determine, since the latter, in nature, remain on land after metamorphosis for one to two years as "red efts" and, when raised in the laboratory in terraria, do not take food for some time, and later show considerable individual variations in feeding response and growth rate.

As far as could be determined from the observation of the living animals, both the metamorphic and the growth reactions to pituitary stimulation were identical in triploid and diploid animals. Ten weeks after the first implant the average length of ten diploid animals was 43.6 mm., that of nine triploid animals was 42.7 mm. Under the conditions of these experiments the additional growth hormone thus failed to produce greater stimulation in the triploids.

With the addition of more sets of chromosomes the viability decreases. Tetraploid as well as pentaploid larvae are less vigorous than triploids and usually develop ascites (Fig. 6: 2), which may increase with age or disappear completely later on. In general, their reactions to mechanical stimulation are slower, and the food intake is more or less reduced. In one pentaploid larva, in which the progress of digestion of *Enchytraeus* worms was more closely watched, it was definitely slower than in the diploids, as measured by the rate of passage through the stomach and intestine.

A physiological effect which seems to be typical for young pentaploid larvae of *Triturus viridescens* is a greater susceptibility to a 1:5000 solution of chloretone, which is used as an anesthetic during photography. Prolonged exposure to this solution has no ill effects on diploid larvae, while two pentaploids showed the typical effects of an overdose of chloretone, characterized by a bending of the main stems of the gills and an almost complete reduction of the gill branches. In both cases no recovery took place, and the general condition of the animals made it necessary to preserve them.

The rate of heart beat was measured repeatedly in a tetraploid and several pentaploid larvae and was found to be approximately normal. The single pentaploid *Triturus pyrrhogaster* observed so far was definitely more vigorous than pentaploids of *T. viridescens*. It never developed ascites and reacted more promptly to various forms of stimulation. It is quite probable that in this species both a decrease and an increase in chromosome number have less effect than in others.

Detailed observations have been made on heteroploid parthenogenetic tadpoles of *Rana nigromaculata* by Kawamura (1939a). He gives his animals the following rating with regard to viability: (1) diploids, (2) triploids and tetraploids, (3) haploids and hexaploids. It must be mentioned, however, that the majority of all parthenogenetic tadpoles in his experiments were very abnormal, regardless of chromosome number.

There is practically no information available on the physiological effects of polyploidy in triploid and tetraploid races of arthropods. Their general viability may be assumed to be normal, since they compete successfully with the diploid races. Artom (1925) merely mentions that in *Artemia* tetraploidy has "important physiological manifestations." I have not been able so far to find an elaboration of this general statement. Vandel (1934) notes that in the isopod, *Trichoniscus elisabethae*, one triploid male lived for two and a half years while diploid males rarely reach their second year.

The rapidly growing literature on the physiological effects of polyploidy in plants will be reviewed briefly in the concluding section, since it suggests various lines of future investigations with animals. In connection with the observations on polyploid salamander larvae just mentioned, it is interesting to note here that haploid plants are also less viable as a rule, that tetraploid individuals may show greater vigor than the diploid (e. g., *Cuthbertia*, Giles, 1942; *Sedum*, H. E. Smith, 1943), while octoploid plants are generally weaker (e. g., *Nicotiana*, Greenleaf, 1938; H. H. Smith, 1943) or cannot be obtained at all (*Datura*, Blakeslee, 1941).

(d) "Qualitative" effects

The effects of heteroploidy on amphibian development discussed so far have been primarily quantitative, largely direct consequences of changes in cell size. Are there also modifications of a more qualitative character, striking abnormalities of development which might be considered as typical for the various changes in chromosome number? The distinction between quantitative and qualitative changes is, of course, often arbitrary. A modification of the proportions of the body or of certain organs, for instance, is based on quantitative alterations that have been of different magnitude in different dimensions. The end result, however, as expressed in the appearance of the developing embryo or larva, is clearly qualitative. The same reasoning applies to changes in the size of single organs, changes which appear purely quantitative when considered alone, but qualitative when viewed from the standpoint of the final effect, which is a distinct pathological condition.

TABLE 9

Abnormalities found in haploid embryos and larvae of amphibians

	SPECIES	AUTHOR
Broader head and body	*Triton taeniatus*	P. Hertwig, 1916, Baltzer, 1922, Fankhauser, 1937a (Fig. 6)
	Triton palmatus	Fankhauser, 1937a (Fig. 7)
Dorsal flexure of body, widening of tail	*Rana pipiens*	Rugh, 1939
Shorter gills	*Bufo, Rana*	G. Hertwig, 1913
	Triton taeniatus	O. Hertwig, 1913, P. Hertwig, 1923
	Triturus viridescens	unpublished
Deformed lower jaw	*Triturus viridescens*	unpublished
	Triturus pyrrhogaster	Fankhauser, 1937a, Kaylor, 1940a
Circulation seldom functional	*Rana pipiens*	Porter, 1939
Neural plate one-third shorter	*Rana pipiens*	Porter, 1939
Microcephaly	*Rana fusca*	Dalcq, 1932
	Rana pipiens	Rugh, 1939
Abnormal development of brain	*Rana pipiens*	Porter, 1939
	Triton taeniatus	P. Hertwig, 1923
Small or abnormal eyes	*Rana pipiens*	Porter, 1939
	Rana fusca	Dalcq, 1932
	Triton taeniatus	P. Hertwig, 1923, Böök, 1941
	Triton palmatus	Fankhauser, 1937a

The main types of abnormalities that have been noted specifically in haploid amphibian embryos and larvae are summarized in Table 9. Most frequent are changes in body proportions, shortening of the gills, and deficiencies in the nervous system, particularly in the brain and the eyes. These last mentioned deficiencies are perhaps all connected with difficulties in gastrulation and consequent deficient induction in the head region. Two points must be emphasized: (1) all these abnormalities also appear in diploid embryos, although more rarely; and (2) among the haploids they appear more or less frequently and vary greatly in degree. They are not constant symptoms always associated with haploidy, except perhaps in certain species, e. g., the shortening of the neural plate and the abnormal development of the brain and eyes in *Rana pipiens* embryos, according to Porter (1939). As a whole, the abnormalities are less frequent and less severe in newt embryos than in those of frogs, as was emphasized by O. Hertwig (1913) and has been substantiated by more recent observations on species of *Triturus*. Some haploid newt larvae are completely normal in appearance as long as they live. Whether or not any particular abnormal condition occurs in anurans but not in urodeles, or vice versa, remains an open question.

Triploid salamander larvae show the same types of abnormalities as diploid larvae, and with about the same frequency. No typical morphological peculiarities have been found. The number of tetraploid larvae observed so far is too small for any general conclusions. The two tetraploids of *Eurycea bislineata* were essentially normal, aside from their slower growth and greater tendency to develop ascites, mentioned earlier. The tetraploid larva of *Triturus viridescens* showed a temporary fusion of the first three digits of the forelimbs which disappeared during later stages. At this time the posterior portion of the tail began to curve to the left and, at metamorphosis, formed a tight coil (Fig. 5: 7).

A curvature of the body axis appears to be typical for older pentaploid larvae. The process usually begins in the tail region and may be caused in part by the excessive width of the tailfin, whose ventral edge bends over in contact with the bottom of the culture dish. Later on the trunk itself shows a more or less pronounced S-curve (Fig. 6: 3–5). Such axial curvatures occur but rarely in diploid larvae and may be typical for animals with four or more sets of chromosomes. This conclusion is supported by the fact that similar, though less extreme, curvatures were found in a pentaploid larva in each of two other species, *Triturus pyrrhogaster* (Fig. 6: 7–8) and *Amblystoma mexicanum*. The cause of this phenomenon may perhaps be found in unequal growth rates of different tissues of the axis, possibly a more rapid elongation of the notochord.

Temporary fusion of some of the digits was also observed in three of the four pentaploids that developed to metamorphosis. In older pentaploid larvae of *Triturus viridescens* the head is definitely more pointed than in the diploid. Altogether, these distinguishing characteristics of larvae with higher chromosome numbers seem to be primarily due to local disturbances of growth patterns.

Changes of a more qualitative nature have also been described in polyploid arthropods. In tetraploid embryos of *Artemia* the outer margin of the head is straight instead of rounded as in the diploid (Artom, 1927). Octoploid *Artemia* have a shorter caudal fork with fewer bristles; higher salt concentrations, which shorten the fork of diploid animals, cause it to be completely absent in the octoploid (Gross, 1932). Triploid *Drosophila* differ from the diploid in the proportions of their body rather than in size and are characterized by a stocky build (Dobzhansky, 1937). Vandel (1927) notes that triploid individuals of the isopod *Trichoniscus* have a purplish color, while the diploids are orange or light brown. Triploid females of the [illegible] *Habrobracon* are often abnormal in appearan[illegible] R. Whiting, 1928; Torvik, 1931) and ma[illegible] irregular abdominal sclerites (Inaba, 193[illegible]

Changes in the proportions of various org[illegible] frequently noted in polyploid plants. In [illegible] the organs of tetraploids are coarser (cf. [illegible], 1938). The leaves, in particular, are broa[illegible]d thicker (cf. Müntzing, 1936), as was alrea[illegible]- tioned by Winkler (1916) for tetraploid [illegible] to seedlings. This change in shape can [illegible]ed back to the leaf initials, which are b[illegible]nd maintain this difference throughout [illegible]ny (maize, Randolph, Abbe, and Einset, 1[illegible]*ca rosea*, Cross and Johnson, 1941). In *Da*[illegible] is a progressive shortening and thickenin[illegible] capsules from the haploid to the octoploid [illegible] tion (Blakeslee, 1941). The shape of the fr[illegible] also modified in tetraploid cucurbits (Sinnott [illegible] Blakeslee, 1938; Shifriss, 1942). Shifriss a[illegible] noted an accentuated serration of the leaf margin in *Cucumis*.

Octoploid plants are frequently abnormal. In *Nicotiana* they show general monstrosity; the dying leaf tips in particular demonstrate that octoploids are close to the upper end of the range of chromosome numbers compatible with development (Greenleaf, 1938). Microscopical study reveals a general disorganization of the cells and tissues in parts of the leaves (H. H. Smith, 1943).

6. Effects on sex differentiation

From the beginning of these studies on polyploidy in amphibians, it was hoped that they might throw some light also on the interesting and controversial subject of sex determination. In contrast to the great volume of work devoted to the embryology and physiology of sex differentiation in this class of vertebrates, the number of papers dealing with the genetics of sex is very limited. There are several good reasons for this: lack of knowledge of heritable variations which would offer an approach through studies on sex linkage, absence of clear-cut visible differentiation of the sex chromosomes, and considerable lability of the genetic sex, which is easily modified by nongenetic factors, at least in some species. Much of the work is still concerned with the primitive question whether the male or female is heterogametic.

The available evidence on the genetical basis of sex is derived mainly from the following sources: (1) Breeding experiments with occasional hermaphroditic frogs and with "differentiated" and "undifferentiated" local races, the results of which are most easily explained on the assumption that the male is heterogametic, XY, the female homogametic, XX (Crew, 1921; Witschi, 1923, 1929, 1934).

(2) Investigation of the gonads of diploid parthenogenetic tadpoles and frogs that lived beyond the stage of sex differentiation (Loeb, Parmenter, Kawamura; cf. review in Tyler, 1941). Since both males and females have been found, the facts derived from this source do not support the assumed female homogamety without some supplementary hypothesis involving the ontogenetic lability of the original sex.

(3) Experiments on sex reversal have furnished the most decisive information in two instances. Removal of the testes of male toads allows the normally present rudimentary ovaries or Bidder's organs to produce mature ova, which may be fertilized by spermatozoa from normal males. According to Ponse (1930, 1941) the offspring from such crosses are all males, a fact which strongly suggests male homogamety in toads. In the salamander *Amblystoma*, an ovary of a genetic female may be completely transformed into a testis under the influence of a grafted testis that was transplanted as a gonad rudiment in an early embryonic stage and is finally removed after transformation of the host gonad has taken place. If a sex-reversed female is mated with a normal one, females and males appear in the offspring in the ratio of three to one. This can be explained on two assumptions, (1) that the female is heterogametic, WZ (or XY), and (2) that WW (or YY) individuals are viable and normal females (WZ × WZ = 1 WW + 2 WZ + 1 ZZ). Actually, it could be shown that one-third of the female offspring are of WW constitution, since they produce female offspring exclusively when mated to normal males, while the remaining two thirds give a normal sex ratio (Humphrey, 1942a, b, 1945).

The value of polyploid individuals in the study of sex determination has been amply demonstrated by the work of Bridges on *Drosophila* intersexes and "supersexes," which are the product of abnormal combinations of sex chromosomes and sets of ordinary chromosomes, or autosomes. Triploid flies are either normal females or intersexes, but never normal males, since the normal ratio of one X-chromosome to two sets of autosomes that is present in diploid males cannot be obtained. Investigation of the gonads of the first four triploid individuals of *Triturus viridescens* that were raised to metamorphosis at once indicated that the sex chromosome mechanism of salamanders is different from that of the fruitfly, since one animal possessed normal appearing testes, while the other three contained under-developed ovaries that were much smaller and less advanced in differentiation than those of diploid controls. The total number of germ cells was reduced to about one-third of the normal (Fankhauser, 1940a). This situation is similar to that found in moths, where triploids are either normal males or females with rudimentary ovaries or with more or less intersexual gonads. For moths, the heterogamety of the females has been established beyond doubt previously through studies on sex-linkage (cf. the review by Cockayne, 1938). The conclusion was obvious, therefore, that in newts also the female possesses an unequal pair of sex chromosomes (WZ), while the male is homogametic (ZZ).

Since the time of publication of this first account many more triploid larvae of *Triturus viridescens* have been raised to metamorphosis for a detailed study of their gonads, a study now in progress. Some of these animals are spontaneous triploids that either have normal appearing testes, or, in the majority of cases, more or less rudimentary ovaries. The far greater number of triploids were experimentally induced by cold or heat treatment of eggs. These induced triploids are practially all females with rudimentary ovaries; only two males have been found so far in a total of over forty animals (Griffiths, 1941; and unpublished observations).

These facts can be explained most easily by the assumptions that the female sex is heterogametic, and that the first meiotic division is equational for the sex-differentiating segments of the W and Z (or X and Y) chromosomes in most of the eggs. The second maturation spindle would thus usually contain a W and a Z chromosome, and suppression of the second maturation division by cold or heat would produce almost exclusively eggs of the constitution WZ which, fertilized by normal Z-bearing sperms, would give rise to WZZ individuals (cf. Fankhauser, 1942).

For a complete analysis of the influence of triploidy on sex it would be essential to study the later development of the gonads. The initial difficulties encountered in the raising of metamorphosed newts into the red eft stage have largely been overcome at present. Furthermore, older gonads are available in the pituitary-implanted, semi-permanent larvae mentioned earlier, where the reactions of the gonads to excessive pituitary stimulation may be studied. A preliminary survey of these slides has shown that the triploid ovaries reacted differently from the diploid as regards both size and structure.

Because of the probable existence of opposite sex determining mechanisms in different taxonomic groups of amphibians it was important to study the effects of triploidy in other species of salamanders. In *Triturus pyrrhogaster*, sex differentiation is not always clear-cut at the time of metamorphosis. Only two cold-induced triploids could be sexed so far. Both possessed ovaries of normal or approximately normal size and histological appearance (unpublished observations of Rita C. Watson). This is in good agreement with Kaylor's findings (1943) that a triploid animal of possibly androgenetic origin had larger ovaries than the controls. More observations are needed to demonstrate conclusively that the gonads of this species react to triploidy in a different way from those of the common eastern newt.

A number of spontaneous triploid larvae of the two-lined salamander, *Eurycea bislineata*, which in nature metamorphoses during the third year, were raised to ages ranging from five to nine months. Four possessed normal testes; five had underdeveloped ovaries or rudimentary gonads of questionable sex. A detailed study of these cases has not yet been made.

As soon as Humphrey announced the demonstration of female heterogamety in *Amblystoma* on the basis of abnormal sex ratios in the progeny of sex-reversed genetic females, it appeared highly desirable to test the effects of triploidy in the same species. The axolotl offers the added advantages of being easily raised to sexual maturity in the laboratory and of having been subjected to a far-going experimental analysis of the phenomena of sex differentiation by Humphrey and others. Refrigeration experiments with axolotl eggs proved at once successful in inducing triploidy (Fankhauser and Humphrey, 1942), and a considerable number of triploids have been obtained, some of which are being raised. A preliminary check of the gonads shows that females again predominate. However, males appear more frequently than in experimental triploids of *Triturus viridescens*, a fact which indicates that the first maturation division may be reductional for the differential segments of the sex chromosomes in a considerable percentage of the eggs. In older triploids the condition of the ovaries varies greatly between individuals and may approach the normal in size and differentiation. Whether or not the later development of triploid testes is normal has not been established as yet.

Theoretical considerations concerning the genetics of sex in salamanders in general would be premature before the available material, including the gonads of tetraploid and pentaploid individuals, has been analysed in detail and more cases have been added. Interesting information may be expected from triploid axolotls with different combinations of sex chromosomes, viz., WZZ, WWZ, and WWW, all of which should be obtainable by refrigerating eggs from the offspring of sex-reversed females.

The possibilities of this approach to the analysis of sex determination in amphibia will not be adequately utilized until it is applied to frogs and toads. The only information on triploid anurans available so far is that obtained by Kawamura (1939b, 1940) on five parthenogenetic individuals of *Rana nigromaculata* and *Rana japonica*, including four advanced tadpoles and one metamorphosed frog. Two of these contained rudimentary ovaries; three possessed more abnormal gonads with few or no germ cells. The interpretation of these observations is not clear, since three of the four diploid parthenogenetic frogs also had degenerated or under-developed ovaries and because, furthermore, most of the parthenogenetic individuals were abnormal in various other respects. Kawamura suggests that abnormal trophic conditions exist in all parthenogenetic animals, to which a triploid constitution of the tissues adds further disturbances of the physiological conditions that interfere with the normal growth of the ovaries.

This survey of the influence of changes of chromosome number on sex would not be complete without a mention of the conditions found in haploid or partially haploid animals. The haploid *Triton taeniatus* that developed from an egg fragment containing a sperm nucleus and was raised to metamorphosis (Baltzer, 1922) contained small but unmistakable ovaries (Fankhauser, 1938b). This fact agreed with the expectation based on the *Drosophila* type of sex determination with female homogamety. No other pure haploids have been raised sufficiently far since then; however, several advanced haploid-diploid mosaic individuals have been examined. In one case (*Triturus pyrrhogaster*, Kaylor, 1943) in which haploid and diploid cells were mixed rather irregularly, the right gonad was a normal ovary, the left, possibly haploid, gonad a poorly developed ovary. In two bilateral haploid-diploid mosaic larvae of *Amblystoma* the gonad on the haploid side was a testis (Humphrey and Fankhauser, 1943). One of these was a gynandromorphic animal in which the diploid gonad on the right side, originally an ovary, had been transformed almost completely into a testis under the influence of the male gonad on the haploid side.

If we assume female heterogamety to be the rule among salamanders, androgenetic animals (with a paternal set of chromosomes) would all be expected to be males. The occurrence of ovaries in an androgenetic newt might be explained by some special supplementary hypothesis as well as by invoking the modifying action of some nongenetic factor. In any interpretation we have to keep in mind constantly the apparently narrow margin between the male and female sex balance in amphibians and the close homology between the W and Z chromosomes, demonstrated by the fact that, in *Amblystoma*, WW and ZZ individuals are fully viable and identical in all respects except sex.

C. CHANGES INVOLVING ONE OR MORE INDIVIDUAL CHROMOSOMES ("ANEUPLOIDY")

Individuals with one or more chromosomes added to the normal diploid complement, or with one or more chromosomes missing, are found rather frequently in plants. In the jimson weed, *Datura*, it was early shown that the addition of each individual chromosome of the haploid set of twelve has different characteristic effects on the appearance of the plant, so that twelve distinct types of "trisomic" plants occur (Blakeslee, Belling, and Farnham, 1920; Blakeslee and Belling, 1924). Similar observations were made later on trisomics of *Nicotiana sylvestris* (Goodspeed and Avery, 1939), in tomatoes (Lesley, 1928), and in maize. Aneuploids with two or more extra chromosomes are in general less viable or fail to appear altogether. As the number of additional chromosomes is increased to the point where they constitute an almost complete third set, the plants again become vigorous since, in such hypo-triploid plants, the total balance of genes approaches the normal sufficiently to be compatible with normal development. However, different species of plants vary greatly in their susceptibility to chromosome unbalance; in cultivated varieties of hyacinths, for instance, most aneuploid chromosome numbers between the diploid (sixteen) and the tetraploid are known (de Mol, 1921; Darlington and Mather, 1944).

Among animals, aneuploidy is a much rarer phenomenon. It has been studied most extensively in *Drosophila*, where the effects of changes involving single chromosomes again depend on the kind of chromosome involved and are closely related to its size. Addition of a small fourth chromosome produces slight changes in the external appearance of the flies, e. g., in the shape of the wings and bristles, while subtraction of the same chromosome causes changes in an opposite direction as well as a pronounced retardation of development and decrease in viability. A third X-chromosome greatly reduces the viability of the larvae and pupae and causes modification of various structures in the surviving adult flies. Flies with one of the large second or third chromosomes added or missing have not been found so far. Presumably they are not viable because of the serious disturbance of the normal balance of genes (cf. Li, 1927).

In species with higher haploid chromosome numbers than *Drosophila*, changes involving a single chromosome would be expected to have less serious consequences. A strain of the grasshopper, *Trimerotropis citrina* (N = 12), was found to carry an extra first chromosome, apparently without striking changes in viability or appearance (Carothers, 1941). In another species of grasshoppers, *Mecostethus grossus*, Callan (1941) found one male, externally normal, in which the third largest autosome was present three times in all mitoses examined. In several species of American land snails, with haploid chromosome numbers ranging from seventeen to thirty-one, individuals or races with 2N + 1, 2N − 1, or 2N − 2 chromosomes occur (Husted, 1943).

Among our salamander larvae six aneuploid individuals have been found so far. One larva of *Triturus viridescens*, developed from an untreated egg, possessed twenty-four chromosomes (2N + 2). It was delayed in development and characterized by a large flat head, small eyes, and poor circulation; it never fed. Both the pigment cells and the blood cells of the living larva were larger than normal. The tailtip regenerated very slowly and showed an irregular, ragged edge. In addition, heart and viscera showed complete situs inversus. Another aneuploid individual of the same species, a hypo-diploid (2N − 3), was much retarded in development, very abnormal from the neurula stage on, and died early. There was pronounced microcephaly, grossly defective circulation, and general deformity of the trunk and tail.

A single hyper-diploid individual (2N + 3 or 4) appeared among larvae of *Triturus pyrrhogaster* that developed from refrigerated eggs (Fankhauser, Crotta and Perrot, 1942). It showed extreme microcephaly and edema along with other abnormal features (Fig. 7: 6). Three hypo-diploid larvae (2N − 3 or 4) were produced in refrigeration experiments with axolotl eggs. All three were abnormal and inviable.

Kawamura (1939a) found a single hyper-diploid individual (probably 2N + 4) among 413 parthenogenetic larvae of *Rana nigromaculata*. It too was clearly abnormal, with strongly curved body and deformed tail.

Although the number of aneuploid amphibian larvae observed so far is small, the fact that all have been abnormal and non-viable seems to indicate that either addition or subtraction of two or more chromosomes is incompatible with normal development. On the other hand, none of the various abnormalities shown by the aneuploids were distinctive, since they also occur among diploid larvae. It is possible, however, that the particular combination of symptoms shown by each larva was typical for its chromosome constitution, because they all differed from one another in their appearance.

Zygotes with unbalanced chromosome complements may be formed more often than is indicated by the small number of aneuploid larvae identified so far. On the one hand, trisomic individuals, with a single chromosome present in triplicate, might be perfectly normal in appearance and viability, as they seem to be among grasshoppers, and would thus readily escape discovery. On the other hand, more extreme unbalance may lead to death at an early embryonic stage and account for a part of the "normal" mortality among amphibian embryos.

Most of the aneuploid plants described have been found among the offspring of triploids, in which meiosis produces spores with various abnormal chromosome combinations. There is no indication so far that any of the aneuploid salamander larvae were derived from a triploid parent, since they occurred singly among normal, diploid larvae, while a mating of a triploid with a diploid should produce a majority of offspring with irregular chromosome numbers. To date, meiosis has been studied in a single triploid salamander, the adult male newt discovered by Böök (1940, 1944). It showed the irregularities typical for autotriploid plants, with formation of univalents and trivalents in addition to bivalents. At metaphase II anywhere from four to twenty-one chromosomes were counted. However, there seemed to be a definite tendency towards formation of spermatids with an approximately haploid chromosome number. Many spermatids underwent pycnosis or developed into abnormal spermatozoa.

D. PARTIAL OR MIXED HETEROPLOIDY: CHROMOSOME MOSAICS

In addition to completely heteroploid amphibian larvae, individuals occur with two or more different chromosome numbers in different parts of the body, or in different cells in a single organ. This situation is of interest because it allows the close comparison of tissues with different chromosome numbers in a single individual and, furthermore, makes it possible to study the question whether certain effects of abnormal chromosome complements may be modified by the presence of normal, diploid cells or organs. Usually a part of the body of such mosaics is diploid; in some cases, however, all chromosome numbers are abnormal. Only two different kinds of chromosome complexes may be present, usually differing from one another by one or more complete sets ("euploid" mosaics). Or the body may represent a complex mixture of various, mostly aneuploid, numbers, which as a rule are the consequences of multipolar mitoses in early cleavage.

On this basis the chromosome mosaics may be divided into three groups: (1) euploid mosaics, in which each of the two chromosome numbers present is found in large areas of the body, or in large numbers of cells; (2) predominantly diploid individuals with one or more small polyploid areas; and (3) complex mosaics with highly irregular chromosome complements. Transitional conditions between these three groups also occur, but most cases may be classified without difficulty.

1. *Euploid mosaics with wide distribution of two chromosome complexes ("chimeras")*

Table 10 shows that among amphibian larvae such mosaics occur spontaneously as well as in various types of experiments, particularly after treatment of eggs to induce haploidy. Consequently, the majority of mosaics are partly haploid, partly diploid. Various other combinations have also been found, such as haploid/triploid, diploid/triploid, etc.

Among the haploid/diploid larvae that have been studied more closely, one may again distinguish various types depending on the relative proportions of haploid and diploid cells and on the topographical arrangement of these cells. Some are predominantly haploid; in others, haploid and diploid cells occur with about equal frequency. In the latter, the body may be haploid on one side and diploid on the other, as in tadpoles developing from dispermic eggs of the frog and in some spontaneous and cold-induced mosaic salamander larvae, or the two kinds of cells may be found mixed irregularly in different parts of the body, as described, for instance, in a mosaic larva of *Triturus pyrrhogaster* (Kaylor, 1943). Various intermediate conditions occur, adding to the complexity of the situation. With the exception of bilateral mosaics, it is very unlikely that the same pattern of chromosome numbers will be found in two different individuals.

TABLE 10

Types of chromosome mosaics ("chimeras") found among amphibian larvae

SPECIES	ORIGIN	NUMBER AND TYPES OF MOSAIC LARVAE	AUTHOR
Rana fusca	parthenogenesis	7 haploid/diploid,	Hovasse, 1922
		4 haploid/diploid,	Parmenter, 1940
		3 diploid/triploid	
	polyspermy	regularly haploid/diploid	Herlant, 1911
Rana pipiens	parthenogenesis	3 haploid/diploid	Parmenter, 1933
		1 diploid/triploid	
	androgenesis	1 haploid/diploid	Porter, 1939
		1 haploid/tetraploid	
		1 diploid/triploid	
Rana palustris	parthenogenesis	1 haploid/diploid	Parmenter, 1933
		1 diploid/triploid/tetraploid	
Rana nigromaculata	parthenogenesis	8 haploid/diploid	Kawamura, 1939a
		3 haploid/triploid	
		1 haploid/pentaploid	
		1 triploid/hexaploid	
Triturus viridescens	spontaneous	1 haploid/diploid	Fankhauser, 1941b
		1 haploid/triploid	
		1 diploid/hypertriploid	
	cold treatment	6 haploid/diploid	Griffiths, 1941
		1 haploid/triploid	
		1 hyper-diploid/triploid	Fankhauser, 1942
		1 haploid/diploid	
Triturus similans	cold treatment	2 haploid/diploid	Costello, 1942
Triturus pyrrhogaster	androgenesis	1 haploid/diploid	Kaylor, 1940a, 1943
Eurycea bislineata	spontaneous	3 haploid/diploid	Michalski, 1942
Axolotl	spontaneous	2 haploid/diploid	Humphrey and Fankhauser, 1943, and current experiments
	cold treatment	2 haploid/diploid	
		1 triploid/pentaploid	
		1 diploid/pentaploid	

The mechanism responsible for the mosaic condition is definitely known in a few instances only. In dispermic frog's eggs, the chromosome pattern is determined by the simultaneous division of the diploid fusion nucleus and the accessory sperm nucleus which remains separated from the former. Haploid and diploid cells, as well as cells with both a haploid and a diploid nucleus are formed during early cleavage, which is more or less irregular. The presence of binucleate cells leads to various complications later on, including abnormal mitoses and failure of further cell divisions in that area.

As a whole, bilateral mosaic larvae may be recognized more easily than other types because of the asymmetrical development of the body, which is curved towards the haploid side or shows delayed differentiation of that side. In some cases the difference in the number and size of the melanophores in corresponding areas is also very striking. Differences in pigmentation are particularly obvious in mosaic axolotl larvae derived from matings between dominant black and recessive white individuals which differ in a single pair of genes, if the chromosome set on the haploid side is contributed by the white parent; under these circumstances it is also possible to determine within limits the mode of origin of the mosaic condition. In both cases studied so far the haploid set was paternal, either brought in by a second sperm nucleus which divided independently (dispermy), or derived from an early division of a single sperm nucleus into two haploid nuclei one of which fused with the egg nucleus to produce the diploid side ("partial fertilization").

The possible modes of origin of parthenogenetic mosaic larvae have been discussed by Parmenter (1933) and Kawamura (1939a, pp. 202, 206, 208), who consider various mechanisms: duplication of the haploid chromosome set in one or more blastomeres during early cleavage through a monocentric mitosis, retention of a second set of maternal chromosomes during maturation followed by a delayed fusion with one of the descendants of the haploid egg nucleus, etc.

The fate of mosaic larvae varies greatly and is probably determined in part by the proportion and distribution of the types of cells with different chromosome complexes. Both bilateral and more irregular mosaics may survive to metamorphosis. An example of the first type, described by Griffiths (1941), is given by the haploid/triploid *Triturus viridescens*, which was predominantly haploid on the left side. Kaylor's (1940, 1943) haploid/diploid mosaic of *Triturus pyrrhogaster* is a representative of the second type. The viability is thus much improved over that of haploids, a fact which offers possibilities for the future analysis of the causes of haploid nonviability. Careful study of a number of mosaics may show whether their viability is dependent on the diploid constitution of any particular organ or tissue (cf. King and Slifer, 1934, p. 609). Furthermore, mosaics may survive past the stage of sex differentiation to furnish more material for the investigation of the sex of haploid gonads (cf. p. 101).

In this connection it is of interest that haploid/diploid mosaics may also be produced artificially by uniting complementary parts of a haploid and a diploid gastrula (Hadorn, 1935, 1937). Some of the conditions obtaining in such "chimeras" can also be reproduced by connecting a haploid embryo with a diploid in parabiosis in early tailbud stages (Kaylor, 1940b).

The literature on chromosome "chimeras" and gynandromorphism in other animals will be discussed in another publication.

2. *Diploid animals with small polyploid areas*

Amphibian larvae of this type may easily escape detection unless the tailfin contains a polyploid sector. So far, only two diploid larvae have been found in which the fin included a small tetraploid area (*Triturus pyrrhogaster*, Fankhauser, Crotta, and Perrot, 1942). The study of complete serial sections through numerous larvae and animals in metamorphosis has not furnished any evidence for such limited, partial polyploidy. Various organs of adults should be investigated with regard to their chromosome complement; however, it does not seem likely that certain organs or tissues are regularly polyploid, or at least partly polyploid ("polysomaty"), a condition found in many plants and insects and also described for the liver of the rat (Beams and King, 1942; Sulkin, 1943; Biesele, 1944).

3. *Complex mosaics with irregular chromosome numbers*

("Poikiloploidy," Levy, 1920b; "multiform aneuploidy" Böök, 1944).

In contrast to larvae possessing cells of two different, usually euploid chromosome constitutions, mosaic animals of this category show a wide range of irregular chromosome numbers in their cells. In the tailfin of parthenogenetic frog tadpoles Levy (1920b) found mitoses with anywhere from eight to twenty-four chromosomes, while haploid and diploid cells were very rare. This observation has not been duplicated in more recent work by various investigators; in any case there is no evidence for a general lability of the chromosome number in the tailfin.

There are obvious reasons why larvae with irregular chromosome numbers in a large proportion of their cells should be rare, although an irregular distribution of chromosomes may be expected whenever abnormal and particularly multipolar mitoses take place during cleavage or later stages of development. The fact is well established that the development of an egg does not proceed normally beyond the gastrula stage if multipolar mitosis occurred at the first or a later cleavage division. This was first demonstrated by Boveri's (1902, 1907) work on dispermic eggs of sea urchins, where the first cleavage mitosis usually has three or four poles between which the chromosomes are distributed at random.

Multipolar mitoses are frequently found in eggs or egg fragments of salamanders undergoing androgenetic development, i. e., from which the egg nucleus has been removed. Fertilization in urodeles is normally polyspermic, but the further development of the accessory sperm nuclei is arrested at the time of the first division of the diploid fusion nucleus through some inhibiting influence originating from the diploid mitotic system (Fankhauser, 1932a; Fankhauser and Moore, 1941a). When this inhibiting mechanism is removed, some of the accessory sperm nuclei divide independently. However, the nuclear and centrosomal components of the mitotic cycle are frequently out of gear, so that various types of abnormal mitosis are found. As a result, relatively few egg fragments or operated eggs develop into purely haploid embryos. The mortality is particularly high during cleavage and in the blastula and gastrula stages. When preserved at the critical stage, such eggs usually show a mosaic of irregular chromosome numbers in most or all of the dividing cells; frequently they also contain cells with asters but without chromosomes (egg fragments of *Triturus viridescens* and *Triton palmatus*, Fankhauser, 1932b, 1934b; whole eggs of *Triturus viridescens*, Fankhauser and Kaylor, 1935; Fankhauser and Moore, 1941b; Kaylor, 1941).

In egg fragments of *Triton palmatus* a more detailed analysis of the composition of the abnormal chromosome complexes was possible than in dispermic sea urchin eggs, because of the large size of the cells and chromosomes and the striking morphological individuality of the latter. In many abnormal sets, although they contain more than the haploid number of chromosomes, certain chromosomes are completely absent while others are represented two or three times, a situation creating an extreme disturbance of the normal balance of the genes. Some complements with the normal haploid chromosome number were also found to be very abnormal in composition. The make-up of such highly abnormal sets reveals a complex mitotic history that must have included a whole chain of abnormal mitoses of various types.

All observations on amphibian eggs are thus still in agreement with Boveri's conclusion that, from the gastrula stage on, a complete haploid set of chromosomes is required for normal development to take place. This is indicated also by the negative results of experiments to obtain sub-haploid frog embryos by fertilizing eggs with radiated or trypaflavinated sperm and attempting to eliminate some maternal chromosomes from the maturation spindle by mechanical means (Dalcq, 1932). In addition, the actual composition of the abnormal complexes with more than the haploid number of chromosomes provides evidence for Morgan's suggestion (1927, pp. 204, 656) that the presence of some chromosomes in duplicate or triplicate may be as disturbing in its effects on development as their complete absence.

E. GENERAL PROBLEMS

1. The relative unimportance of specific cell size in amphibian development

One of the main results of these studies on heteroploidy in amphibians is the demonstration that embryonic and larval development are relatively independent of cell size. Although the average cell size in a given tissue is typical for the species, the dimensions of the individual building blocks may be changed well beyond the limits of the normal range of variation found in diploid individuals without any serious interference with development. We may say, then, that the complex processes of early vertebrate development and organogenesis may proceed normally, on the whole, not only with cells of the normal size two, typical for the diploid condition, but also with units of the sizes one, three, four, or five.

This finding eliminates one of the hypotheses regarding the relative scarcity of polyploidy among animals repeatedly suggested, most recently by von Wettstein (1940, p. 386). He assumes that the complicated processes of the embryonic development of animals, like gastrulation, must be dependent on such a delicate balance between cell size, cell number, and rate of cell division that any marked change of these values would necessarily lead to disturbances that should be much more serious than in plants, with their simpler conditions of development.

It is quite possible that the detailed microscopical study of pentaploid larvae preserved in various stages of development will show some deviations from the normal path of development. However, there can be no doubt that a typical salamander larva, with all its complex and coordinated activities, can be built from cells that are two and one-half times larger than normal. Whether still larger cells are compatible with normal development is not known. Kawamura's (1939a) hexaploid frog tadpoles were very abnormal; but so were many of his triploid and diploid parthenogenetic larvae. The fact that octoploid races of the brine shrimp *Artemia* occur in nature cannot be taken as a sure indication that octoploid vertebrate embryos are viable, particularly in view of the fact that in plants the upper limit seems to be reached or passed in octoploid individuals.

2. *The maintenance of normal body size in polyploid larvae through adjustment of cell number*

A second striking phenomenon is the absence of gigantism among polyploid salamander larvae, a fact which shows that the typical body size is maintained as far as possible under a variety of disturbing conditions. At every level of polyploidy, from the triploid to the pentaploid, the increase in cell size is compensated by a corresponding decrease in cell number. Therefore, the body size that is typical for the species cannot be determined by a genetically fixed ceiling on cell number, or at least not by this factor alone. Cell number is controlled by other factors the nature of which is not known with certainty as yet, although several possibilities suggest themselves:

(1) Various investigators have proposed that a constant body size could be obtained automatically, irrespective of chromosome number, if the rate of cell division were to change in inverse proportion to cell size. Indirect evidence obtained from the study of the rate of regeneration in triploid larvae, which is normal, does not support this view, as far as triploidy is concerned. The lower growth rate and the slower progress of regeneration in pentaploid larvae demonstrate a lower rate of cell division but do not tell whether this is a primary attribute of the polyploid cells or a secondary consequence of a decreased physiological efficiency of the polyploid organism. It will be necessary to test the rate of mitosis of polyploid cells in tissue culture, where they are removed from any control of the body as a whole.

(2) A second factor is suggested by the important rôle in growth control played by the pituitary. If the production of growth hormone were to decrease more and more as the chromosome number increases, or if polyploid tissues were less reactive to the same concentration of the hormone than the diploid, the size of the body might be kept within normal limits. The preliminary experiments reported in this paper did not show any significant difference in the reactivity of diploid and triploid larvae to implants of adult pituitaries. It will be of great interest in the future to attempt an assay of the various pituitary hormones produced by polyploid animals, since a functional deficiency of the pituitary might also express itself in the development of the gonads.

(3) The maintenance of normal body size may also be an expression of the adaptive power of the amphibian embryo, which is well known for its ability to achieve a normal or nearly normal development in spite of the most drastic attempts of the experimenter to interfere with it. The mechanisms that underly this regulative ability are still unknown. That it also has a controlling influence on the size of the body is strongly suggested by the growth of diploid salamander larvae developed from half-eggs or from isolated blastomeres that, at the time of hatching, are approximately half the normal size but approach the typical size of the species as they reach metamorphosis.

The existence of some regulatory genetic mechanism governing total organ size rather than body size in certain plants has been suggested by Sinnott and Franklin (1943) to explain the normal size of the mature fruit in tetraploid cucurbits. However, the regulation in this case is secondary, since the tetraploid fruit primordium is about twice as large as the diploid, but loses this initial advantage because of a reduced expansion of the cells during the later stages of growth.

3. *The maintenance of normal form of organs through changes in cell shape*

The subordination of individual cells to a more general controlling mechanism is demonstrated with particular clarity when a structure of a polyploid larva cannot reach normal configuration through an adjustment of cell number alone. Where cells are arranged in a single layer to form a small tube, as in pronephric tubules, the thickness of the wall cannot be kept constant, with larger cells, except by changes in their shape. Preliminary observations on pronephric tubules of young larvae have shown that both the size of the cross-section of the tubule and the diameter of its wall are approximately the same in haploid, diploid, and pentaploid individuals. This is accomplished by a progressive flattening of the individual cells with increasing chromosome number so that a cross section of a pentaploid tubule comprises two cells on the average, while in a diploid tubule one may find from three to six. Similar changes in cell shape are found in the epidermis and may be expected in other thin layers of cells. In this connection, mention should again be made of the changes that have been described recently in the shape of the cell of the apical meristem of tetraploid plants (*Vinca rosea*, Cross and Johnson, 1941), although in this case the wider cells of the tetraploid are responsible for the greater width of the stem and of the leaf primordia rather than for the preservation of normal form.

4. *Specific, qualitative effects of polyploidy and their theoretical interpretation*

The existence of qualitative differences between diploid and polyploid plants is beyond doubt, although their importance and frequency have received widely divergent estimates from different workers. According to Darlington (1937), the same chromosome complement always has a qualitative as well as a quantitative effect when represented different numbers of times. Müntzing (1936, p. 281), on the other hand, emphasizes that tetraploid plants are mainly magnified editions of the diploid, although certain differences may occur that are not strictly quantitative. Certain abnormalities that may be classified as qualitative changes have been noted in haploid and pentaploid amphibian larvae. They appear to be caused largely by local changes in growth patterns. However, it is likely that more detailed investigations will bring out more numerous and more varied deviations from the normal condition.

The existence of qualitative differences between polyploid and diploid individuals is of great theoretical interest since, at first sight, the multiplication of all the genes of the complement, maintaining a normal gene balance, would not be expected to change the final effect of the genotype. Various suggestions have been made to explain these qualitative effects. First of all, the possibility should be mentioned that, in polyploid organisms, one may have to differentiate between the action of the genes themselves and that of the total mass of "chromatin," which seems to be mainly responsible for the increase in nuclear and cell size and thus creates different spatial conditions for the activity of the former (cf. Lindstrom, 1936; Goldschmidt, 1937). Special studies of this dual effect of polyploidy are needed, although they may not be very profitable until the relations between genes and "chromatin" are better understood.

Several authors have stated in general terms that qualitative changes may be expected because an increase in chromosome number produces a new genetic system. More specifically, the expression of the genes may be different in a polyploid for any one of the following reasons or a combination of them:

(1) Some genes may produce their maximum effect in double dose, while others do not; in the polyploid, the action of the former would not be enhanced, while the latter would show a cumulative action (Randolph and Hand, 1938, 1940, p. 63; Goldschmidt, 1938, p. 152).

(2) Genes with cumulative action in turn may vary greatly in the extent to which additional alleles will enhance their expression. With some, the increase in total effect may be small; with others, doubling of the gene number may more than double the effect, as in the case of the gene for yellow endosperm color in corn, where the tetraploid shows a fivefold increase in the amount of carotenoid per cell (Randolph and Hand, 1940).

(3) The cytoplasmic substrate with which the gene products finally interact may be limited in amount for some genes, but present in excess for others, a condition which would again produce a differential effect on gene expression in the polyploid (cf. Goldschmidt, 1938, p. 152).

(4) If the diploid is heterozygous for any number

of factor pairs, addition of a third set of genes may change the dominance relations at different loci to different degrees. Some genes, in single dose, are completely dominant over two recessive alleles; others are not. In the tetraploid, on the other hand, if it is produced by chromosome doubling, the dominance relations should be similar to those in the diploid.

5. *Physiological effects of polyploidy*

Recent studies on polyploid plants emphasize more and more the importance of physiological changes produced by the increase in chromosome number. Many of these physiological effects are interrelated or connected with morphological modifications. Brief summaries may be found in Müntzing (1936), Cain (1944, chapters 27 and 28) and O'Mara (1942). Here it will suffice to list some of these observations to demonstrate the character and variety of physiological consequences of polyploidy:

(1) increase in concentration of various important substances, such as vitamin C in tetraploid tomatoes (Sansome and Zilva, 1933) and in triploid apples (Crane and Zilva, 1931; Müntzing, 1936, p. 367), nicotine in tetraploid tobacco (Naguti, Okuma, and Oka, 1939), carotenoid in the endosperm of tetraploid corn (Randolph and Hand, 1938, 1940), sugar, ascorbic acid and colloidal nitrogen in tetraploid cabbage (Barr and Newcomer, 1943), carotene and anthocyanin in flowers of tetraploid snapdragons and other species (Straùb, 1940);

(2) decrease of ash in tetraploid tomatoes (Kostoff and Axamitnaja, 1935);

(3) decrease in osmotic pressure of cell sap in heteroploid mosses (Becker, 1931) and in *Vinca* (Taylor, 1942);

(4) changes in rate of water absorption and transpiration in tetraploid *Vinca* (Taylor, 1942);

(5) changes in the rate of photosynthesis and of carbon-dioxide production per unit of leaf surface (cf. Kostoff, 1938),

(6) changes in photoperiodism (female sterility of tetraploid rye under natural short days of January and February, O'Mara, 1942),

(7) increased resistance to attack by fungus in triploid aspen, *Populus tremula* (Nilsson-Ehle, 1936),

(8) greater adaptability to environmental conditions, particularly to different soils, and thus wider geographic range (cf. Cain, 1944, chapter 29),

(9) change from self-incompatibility to compatibility in fertilization in tetraploid Petunia (Stout and Chandler, 1941).

These observations suggest a multitude of studies on the physiology of polyploid amphibians or other vertebrates, studies which should also include typically animal functions, e. g., the biochemistry of the blood; digestion, excretion, and glandular activity with particular regard to the endocrines; the physiology of the nervous system in the presence of fewer but larger cells, with emphasis on the rate of transmission of impulses, the activity of sense organs, and learning ability. In short, any function in which cell size and cell number may play a rôle would be worth investigating in polyploid individuals. It is unfortunate that tetraploids occur rarely and cannot yet be produced experimentally, since they would constitute more favorable material than triploids because of the greater magnitude of the primary effects.

6. *Sex determination in vertebrates*

The fact seems well established at present that among amphibians both male heterogamety (XY/XX sex chromosomes of frogs) and female heterogamety (WZ/ZZ chromosomes of toads and salamanders) occur. Whether or not there are exceptions to this rule in either or both of the two groups remains an open question. It is not unlikely that opposite sex chromosome mechanisms may be found in related species, as is the case in cyprinodont fishes. Of great interest in this connection are Gordon's (1945) recent observations on *Platypoecilus maculatus*, in which XY chromosomes are present in wild populations and WZ chromosomes in domesticated breeds. These findings suggest the possible existence of geographical races with contrasting sex chromosome mechanisms in some species of amphibians, a condition which would offer an explanation of the observations on *Triton taeniatus* discussed earlier in this paper. The ovarian character of the gonads of the single androgenetic haploid raised to metamorphosis in Switzerland would be in agreement with the expectation based on female heterogamety as found in *Drosophila*. The normal maleness of the single adult triploid found in Sweden, on the other hand, can be accounted for easily on the basis of male homogamety and corroborates our observations on *Triturus viridescens* and other species. However, as long as the exceptional situation of the haploid remains an isolated case it may well find an entirely different explanation.

In salamanders the differentiation of the W and Z chromosomes from the autosomes and from one another has not proceeded very far, as is shown by their morphological identity and Humphrey's discovery that an axolotl of the constitution WW is a viable, normal salamander, identical with a ZZ individual aside from the primary and secondary sex characteristics. The W and Z chromosomes may be largely homologous except for a short differential segment carrying the genes that trip the balance in a male or female direction. Moreover, the normal appearance and activity of the ovaries of a WW female also show that the Z chromosome cannot carry any important female determining factors in its differential segment.

Further work on the sex of polyploid amphibia should also yield information on the relative distribution of male- and female-determining genes in the sex chromosomes and autosomes, a situation which must remain unknown unless the two types of chromosomes can be matched in various polyploid combinations. Although observations on the single class of Amphibia could not provide a sound basis for general conclusions regarding the distribution of "sex genes" in the chromosome complement of vertebrates as a whole, they would in all probability present a closer approach to the situation in birds and mammals than the classical investigations on insects and dioecious plants.

7. *Heteroploidy and cancer*

Deviations from the normal chromosome number have often been described in tumor cells and have been suggested repeatedly as one of the factors responsible for the transformation from the normal to the malignant state. Following Boveri's lead (1914), the importance of multipolar and other abnormal forms of mitosis producing highly irregular chromosome complements was emphasized in earlier investigations. In recent years the occurrence of polyploidy in tumor cells has been given renewed attention and was supplemented by the discovery that endomitosis may produce polyvalent chromosomes that may or may not separate into their component units to increase the total number of chromosomes (cf. Biesele, Poyner, and Painter, 1942). The study of these nuclear phenomena is also particularly significant in the analysis of the early stages of experimental carcinogenesis that mark the transition from the normal to the precancerous condition (Biesele and Cowdry, 1944).

For investigations of this nature amphibians offer obvious advantages, first, because of the large size of their cells and chromosomes, and secondly, because of the knowledge that is already available regarding the effects of multipolar mitosis and polyploidy in normal tissues. Little is known at present concerning the reactions of amphibian tissues to carcinogens (cf. Needham, 1942, p. 239 ff.). Preliminary investigations of the effects of the subcutaneous application of methyl-cholanthrene on the skin of adult newts (*Triturus viridescens*) showed an early hyperplasia of the epidermis in the region of the implant, followed by the appearance of a large swelling that regressed later on, with extensive necrosis in the subcutaneous connective tissue (Hilton, 1942; Crecca and Warner, 1944). The prompt and pronounced reaction of the epidermis offers favorable material for chromosome studies. Whether the effects are temporary or may lead to malignant changes is unknown. In either case they are worth investigating, because of the possible connection between any peculiarities in the reaction to carcinogens on the one hand, and the extensive power of regeneration of adult salamanders and the general theory of organizers in amphibian development on the other, as has been pointed out by Waddington (1935) and Needham (1936, 1942).

Furthermore, whatever the nature of the effects of carcinogens in amphibians, once they are well analysed in diploid individuals it will be possible to apply the substances to polyploids and to compare their reactions with those of the former. This comparison would be of considerable interest from the standpoint of the mechanisms that underlie the early changes leading to tumor formation (cf. Cowdry, 1943), since it would reveal whether the size of the cells, or the quantity of chromosome material present, has any influence on these processes.

8. *Allopolyploidy and "allo-haploidy"*
(hybrid androgenesis)

In plants, doubling of the chromosome number may be superimposed on cross-fertilization between different species to produce "allotetraploid" or "amphidiploid" plants which combine characteristics of the two parent species with general features of tetraploids and represent distinct, fertile, and true-breeding types. No allopolyploid animals have been found in nature or produced by experimental means so far. Refrigeration of freshly cross-fertilized amphibian eggs would be expected to produce triploids with one paternal and two maternal sets of chromosomes. Preliminary experiments with two species of Californian *Triturus* have not yet yielded significant results (Costello, 1942). In this connection it should again be mentioned that, depending on the particular combination of species used, hybridization in amphibians produces diverse results, ranging all the way from viable hybrids to haploid "false hybrids" that develop by gynogenesis with the maternal chromosomes alone. In the latter case, refrigeration of eggs may double the chromosome number from haploid to diploid (cf. Rostand, 1938).

Important results have already been obtained from experiments that are in part the reverse of those producing allopolyploids, viz., cross-fertilization followed by removal of the maternal set of chromosomes producing an androgenetic hybrid or, to use a term corresponding to allopolyploidy, an "allohaploid." The combination of the egg cytoplasm of one species of newt (*Triton*) with a haploid chromosome set of another does not give rise to viable larvae. Development comes to an end at various early stages, depending on the taxonomic relation of the two species used (Baltzer, 1920; P. Hertwig, 1922, 1923). However, in one combination analysed very fully the disharmony expresses itself primarily in a localized area, namely, the head-mesoderm, the breakdown of which causes the death of the embryo (Baltzer, 1930). If other regions of the androgenetic embryo are isolated in the gastrula stage and transplanted to normal, diploid embryos (Hadorn, 1932), or raised in vitro in salt solution (Hadorn, 1934), they may undergo complete histological differentiation. Transplants of epidermis may remain alive for months and, following metamorphosis, develop characteristics that are typical for the maternal species that contributed the cytoplasm (Hadorn, 1936). The conditions of such experiments would be somewhat simplified if a method were available for the induction of chromosome doubling in the "allo-haploid" egg in order to eliminate all disturbances that may arise from the haploid condition as such, rather than from the specific differences between cytoplasm and chromosomes.

SUMMARY

Amphibians are the only vertebrates in which the effects of changes in chromosome number have been studied so far. The results of these investigations are presented in this paper, with particular emphasis on the effects of heteroploidy on embryonic and larval development, and compared with observations on polyploid invertebrates and plants; these comparisons are not included in the summary.

A. Methods of identification of living heteroploid individuals

The chromosome number of young larvae may be determined directly by counts in dividing epidermis cells of the fin in a whole mount of the amputated tailtip. Secondary criteria of changes in chromosome number are: (1) the size of interphase nuclei in epidermis cells and other tissues, (2) the size of erythrocytes and of unicellular glands, (3) the spacing of epidermis and connective tissue nuclei, (4) changes in cell number in lateral line sense organs, (5) the number of nucleoli in interphase nuclei of epidermis cells, corresponding to the number of haploid chromosome sets present (clearly visible in axolotl tailtips only).

Before tailclipping, heteroploid larvae are often recognized by their distinctive pigment pattern, with larger but fewer melanophores as the chromosome number increases.

B. Addition and subtraction of whole chromosome sets (polyploidy and haploidy)

1. Frequency of spontaneous aberrations (Table 3)

Among larvae of the newt, *Triturus viridescens*, triploid individuals appear with a frequency of about 1.8 per cent, pentaploids occupy second place (ca. 0.28 per cent), haploids third (ca. 0.16 per cent). Tetraploid and aneuploid larvae, as well as chromosomal mosaics, occur more rarely. Similar deviations from the diploid chromosome number occur spontaneously in *Triturus pyrrhogaster*, *Eurycea bislineata*, and the axolotl.

2. The origin of spontaneous aberrations

Triploid individuals originate from the fusion of an unreduced, diploid gamete with a haploid one. It is probable that the egg contributes the extra set of chromosomes more frequently than the sperm. Whether tetraploid embryos are produced by the rare union of two diploid gametes, or by somatic doubling in the zygote, is unknown. Pentaploid embryos are most likely produced by the fusion of a tetraploid egg, resulting from complete suppression of both maturation divisions, with a haploid sperm. Paternal inheritance of pigment pattern in one case shows that haploid axolotl larvae may develop by androgenesis. Less conclusive evidence indicates that other haploids develop with the maternal set of chromosomes, by gynogenesis or, possibly, parthenogenesis.

3. Experimental induction of changes in chromosome number

Haploid development of amphibian eggs may be induced by any one of the following methods: (a) parthenogenesis, (b) radiation or chemical treatment of spermatozoa before fertilization, (c) radiation of eggs before fertilization, (d) mechanical removal of egg chromosomes from fertilized eggs, (e) division of fertilized eggs into fragments, (f) application of cold or heat shortly after fertilization, (g) exposure of eggs to hydrostatic pressure.

Triploid embryos have been obtained in several species of salamanders by subjecting eggs immediately after fertilization to cold or heat to suppress the second maturation division, which is in metaphase at this time. Of all the larvae obtained so far from refrigerated eggs of *Triturus viridescens*, 78 per cent were triploid; among the larvae from heat-treated eggs, 71 per cent were triploid (Tables 5 to 8). Tetraploidy has not been induced experimentally so far.

Heteroploid embryos, including hexaploids, have also been obtained as by-products of unknown origin in experiments on parthenogenesis and androgenesis.

4. Primary effects of changes in number of chromosome sets

The size of the nuclei and cells increases approximately in proportion to the chromosome number (Table 2 and Fig. 1). Sufficiently accurate measurements of both nuclear and cell volume have not been made to determine whether the nucleoplasmic ratio remains constant at all levels of polyploidy. In some tissues heteroploid cells also show changes in shape.

5. Secondary effects

(a) *Body size.* The body size of polyploid amphibian larvae at comparable stages of development is always approximately the same, irrespective of chromosome number and cell size, since the latter is compensated by a corresponding reduction in cell number. Haploid larvae as a rule are smaller but show at least partial compensation in cell number.

(b) *Rate of development.* Haploid embryos develop more slowly than diploid. Whether the rates of growth and differentiation are affected to different degrees is not yet known. The growth rate of triploid salamander larvae is normal at first; in later stages of development it may or may not become slightly higher than in the diploid. In triploid *Triturus viridescens* the onset of metamorphosis is often delayed; the mean age at the first molt of 69 diploid animals was 89.4 days, that of 32 triploids was 102 days.

In tetraploid and, particularly, in pentaploid larvae of the same species differentiation, as judged by external features, is only slightly slower than in controls, while the growth rate is greatly reduced. Metamorphosis is delayed as a rule until the larvae have reached approximately the size typical for diploids at this stage.

(c) *Physiological effects.* The viability of haploid amphibian larvae is greatly reduced. Of thousands of haploids, only a few developed beyond the stage when feeding normally begins, and only a single one was raised to metamorphosis. The great majority of haploid larvae develop a more or less severe edema that is held by some to be the main cause of the lowered viability.

The viability of triploid salamander larvae appears to be normal. The few triploid newts that have been raised beyond metamorphosis seem to be as vigorous as the controls, as are some triploid axolotls which have been kept for over two years. Tests of the reactions of older diploid and triploid larvae of *Triturus viridescens* to implantation of adult pituitaries revealed no significant differences in growth rate or in other responses, with the exception of the gonads.

Tetraploid and pentaploid larvae are less vigorous and usually develop temporary ascites. As a whole their reactions are slower. Young pentaploid larvae seem to be more susceptible to the toxic effects of dilute chloretone solutions.

(d) *Qualitative effects.* Haploid embryos and larvae are usually characterized by changes in body proportions, shortening of the gills, and deficiencies in the nervous system, particularly in the brain and eyes. As a rule, these abnormalities are less severe in embryos of newts than in those of frogs.

Triploid salamander larvae do not show any morphological peculiarities. Older pentaploid larvae develop a curvature of the body axis, beginning in the tail and sometimes leading to a tight coiling of the tail and pronounced S-curve of the whole body axis. In older pentaploid larvae of *Triturus viridescens* the head is more pointed than in the diploid. These abnormalities may be caused largely by local changes in growth patterns.

6. Effects on sex differentiation

At metamorphosis spontaneous triploids of *Triturus viridescens* possess either normal-appearing testes or more or less rudimentary ovaries with greatly reduced numbers of germ cells. The gonads of cold-induced triploids almost always are of the last mentioned type. These facts can be explained most easily by assuming that the female sex is heterogametic, and that the first maturation division is equational for the differential segments of the W and Z chromosomes in the great majority of eggs.

Spontaneous triploid larvae of *Eurycea bislineata* also are either normal males or females with rudimentary ovaries. In *Triturus pyrrhogaster*, on the other hand, triploid individuals at metamorphosis may have ovaries of normal size. The later development of triploid gonads has not been studied as yet, except in preliminary observations on axolotls which show that the condition of the ovaries varies greatly between individuals and may approach the normal.

Observations on haploid gonads are limited to four cases: a completely haploid, androgenetic *Triton taeniatus* which had small ovaries; a haploid/diploid mosaic larva of *Triturus pyrrhogaster* obtained in experiments on androgenesis, with a poorly developed, possibly haploid ovary on the left side; and two lateral haploid/diploid mosaic larvae of *Amblystoma*, in both of which the gonad on the haploid side was a testis.

C. Changes involving one or more individual chromosomes ("aneuploidy")

Seven hyper-diploid or hypo-diploid amphibian larvae have been found so far. All were abnormal and non-viable. Apparently, both addition and subtraction of two or more chromosomes are incompatible with normal development.

D. Partial or mixed heteroploidy: chromosome mosaics

1. Chromosomal mosaics or "chimeras" with two different, usually euploid, chromosome complexes in different regions of the body (haploid/diploid, haploid/triploid, diploid/triploid, etc.) occur spontaneously and in various experiments (Table 10). The proportion and the arrangement of the two types of cells vary greatly. Bilateral haploid/diploid mosaics are easily recognized among offspring from matings between dark and white axolotls if the haploid complement is derived from the white parent. As a rule, the viability of haploid/diploid mosaics is much better than that of pure haploids.

2. In two cases only, a small tetraploid area was found in the tailfin of an otherwise diploid larva. Such a condition might actually be more frequent but easily overlooked if the polyploid area were located in another part of the body.

3. Complex mosaics with irregular chromosome numbers result from the abnormal distribution of chromosomes in multipolar mitoses during early cleavage. Such eggs do not develop beyond the gastrula stage. Analysis of the composition of the abnormal chromosome complements shows that the majority are extremely unbalanced, with some chromosomes missing while others are represented two or three times. The presence of a complete, balanced set of chromosomes appears to be indispensable for amphibian development from the gastrula stage on.

E. General problems

1. Embryonic and larval development are relatively independent of cell size and may proceed normally, on the whole, not only with cells of the usual "size 2," typical for the diploid condition, but also with cells of sizes 1, 3, 4, or 5.

2. The adjustment of cell number that maintains an approximately normal body size in polyploid larvae in spite of the increase in cell size shows that the total cell number cannot be irrevocably fixed for the species, even within wide limits. The factors which may control cell number, and thus body size, are discussed briefly.

3. In organs with cells arranged in single layers, as in the tubules of the pronephros, the normal form may be maintained in polyploid larvae by changes in cell shape, viz., a progressive flattening of the individual cells with increasing chromosome number.

4. The theoretical importance of the occurrence of qualitative changes in polyploid organisms is discussed, particularly the question why multiplication of all the genes may produce changes in the expression of some genes and not of others.

5. Some physiological effects of polyploidy in plants are described briefly, since they suggest future physiological studies on polyploid animals.

6. The relations of polyploidy to sex in amphibians are discussed with regard to the problem of sex determination in vertebrates in general.

7. The occurrence and theoretical significance of heteroploidy in tumor cells indicate that diploid and polyploid amphibians may be favorable material for cytological studies of the early reactions of cells to carcinogens.

8. While polyploid species hybrids (allopolyploids) have not been studied in amphibians so far, interesting results have been obtained in experiments in which hybridization is followed by removal of the maternal chromosome set producing an androgenetic hybrid (or "allo-haploid"), with cytoplasm of one species and a haploid chromosome set of another in all its cells.

LIST OF LITERATURE

A. General articles on polyploidy

ARTOM, C. 1928. La polyploidie dans ses corrélations morphologiques et biologiques. *C. R. Soc. Biol. Paris*, 99, réunion plénière: 29–49.

BEAL, J. M. 1942. Induced chromosomal changes and their significance in growth and development. *Amer. Nat.*, 76: 239–252.

BLAKESLEE, A. F. 1941. Effect of induced polyploidy in plants. *Amer. Nat.*, 75: 117–135.

CAIN, S. A. 1944. *Foundations of Plant Geography*, Chapters 26–30. New York: Harper.

DARLINGTON, C. D. 1937. *Recent Advances in Cytology.* 2nd ed. Chapter 6. Philadelphia: Blakiston.

DOBZHANSKY, TH. 1941. *Genetics and the Origin of Species.* 2nd ed. Chapter VII. New York: Columbia Univ. Press.

GOODSPEED, T. H., and M. V. BRADLEY. 1942. Amphidiploidy. *Bot. Rev.*, 8: 271–316.

HEILBORN, O. 1934. On the origin and preservation of polyploidy. *Hereditas*, 19: 233–242.

HUSKINS, C. L. 1941. Polyploidy and mutations. *Amer. Nat.*, 75: 329–346.

LINDSTROM, E. W. 1936. Genetics of polyploidy. *Bot. Rev.*, 2: 197–220.

MÜNTZING, A. 1936. The evolutionary significance of autopolyploidy. *Hereditas*, 21: 263–378.

MULLER, H. J. 1925. Why polyploidy is rarer in animals than in plants. *Amer. Nat.*, 59: 346–353.

SANSOME, F. W., and J. PHILP. 1939. *Recent Advances in Plant Genetics.* 2nd ed. Chapters 5 to 8. Philadelphia: Blakiston.

SHARP, L. W. 1943. *Fundamentals of Cytology.* Chapter 14. New York: McGraw-Hill.

STEBBINS, G. L. 1940. The significance of polyploidy in plant evolution. *Amer. Nat.*, 74, 54–66.

——. 1942. Polyploid complexes in relation to ecology and the history of floras. *Amer. Nat.*, 76: 36–45.

VANDEL, A. 1937. Chromosome number, polyploidy, and sex in the animal kingdom. *Proc. Zool. Soc. Lond.*, 107A: 519–542.

VON WETTSTEIN, F. 1927. Die Erscheinung der Heteroploidie, besonders im Pflanzenreich. *Ergebn. Biol.*, 2: 311–356.

B. Special articles

ARTOM, C. 1923. Il tetraploidismo dei maschi dell' *Artemia salina* di Odessa in relazione con alcuni problemi generali di genetica. *Rend. Roy. Acad. Naz. dei Lincei*, 32: 505–507.

——., 1925. Gigantismo e costituzioni genetiche nell razze e nelle specie tetraploidi. *Riv. Biol.*, 7: 533–555.

——. 1927. Il diploidismo e il tetraploidismo dell' *Artemia salina. Verh. 5th Intern. Kongr. Vererb. Berlin*, 384–386.

——. 1929. Il differenziamento e l'accrescimento degli elementi nervosi dell'*Artemia salina* diploide e tetraploide durante lo sviluppo. *Bull. Ass. Anat.*, 24me réunion: 35–40.

ASTAUROV, B. L. 1940. *Artificial Parthenogenesis in the Silkworm (Bombyx mori* L.). Moscow.

BALTZER, F. 1920. Ueber die experimentelle Erzeugung und die Entwicklung von *Triton*-Bastarden ohne mütterliches Kernmaterial. *Verh. Schweiz. Naturf. Ges., Neuenburg.*

——. 1922. Ueber die Herstellung und Aufzucht eines haploiden *Triton taeniatus. Verh. Schweiz. Naturf. Ges., Bern:* 248–249.

——. 1930. Ueber die Entwicklung des Tritonmerogons *Triton taeniatus* x *cristatus. Rev. Suisse Zool.*, 37: 325–332.

BARBER, H. N., and H. G. CALLAN. 1943. The effects of cold and colchicine on mitosis in the newt. *Proc. Roy. Soc. London, B*, 131: 258–271.

BARIGOZZI, C. 1941. Cytogenetical analysis of two wild populations of *Artemia salina* in connexion with polyploidism. *Proc. 7th Intern. Genet. Congr. Edinb.:* 57–58.

BARR, C. G., and E. H. NEWCOMER. 1943. Physiological aspects of tetraploidy in cabbage. *J. Agric. Res.*, 67: 329–336.

BARTHELMES, A. 1941. Mutationsversuche mit einem Laubmoos, *Physcomitrium piriforme.* I. Morphologische und physiologische Analyse der univalenten und bivalenten Protonemen einiger Mutanten. *Z. ind. Abst. Vererb.*, 79: 153–170.

BATAILLON, E. 1904. Nouveaux essays de parthénogénèse expérimentale chez les vertébrés inférieurs

(*Rana fusca* et *Petromyzon planeri*). *Arch. Entwmech. Org.*, 18: 1–56.

——— and Tchou-Su. 1929. Analyse de la fécondation par l'hybridation et la polyspermie physiologique. *Arch. EntwMech. Org.*, 115: 779–824.

Beams, H. W., and R. L. King. 1942. The origin of binucleate and large mononucleate cells in the liver of the rat. *Anat. Rec.*, 83: 281–298.

Becker, G. 1931. Experimentelle Analyse der Genom- und Plasmon-wirkung bei Moosen. III. Osmotischer Wert heteroploider Pflanzen. *Z. ind. Abst. Vererb.*, 60: 17–38.

Biesele, J. J. 1944. Chromosome complexity in regenerating rat liver. *Cancer Res.*, 4: 232–235.

——, and E. V. Cowdry. 1944. Chromosomal changes in epidermal carcinogenesis. *J. Nat. Cancer Inst.*, 4: 373–385.

——, H. Poyner, and T. S. Painter. 1942. Nuclear phenomena in mouse cancers. *Univ. Texas Publ.* 4243.

Blakeslee, A. F., and J. Belling. 1924. Chromosomal mutations in the jimson weed, *Datura stramonium*. *J. Hered.*, 15: 194–206.

——, J. Belling, and M. E. Farnham. 1920. Chromosome duplication and mendelian phenomena in *Datura* mutants. *Science*, 52: 388–390.

Böök, J. A. 1940. Triploidy in *Triton taeniatus* Laur. *Hereditas*, 26: 107–114.

——. 1941. Induction of haploidy in a cold treatment experiment with egg cells of the salamander *Triton taeniatus*. *Kungl. Fysiogr. Sällsk. Lund. Forh.*, 11, no. 12: 1–16.

——. 1944. Personal communication.

Boveri, Th. 1902. Ueber mehrpolige Mitosen als Mittel zur Analyse des Zellkernes. *Verh. phys. med. Ges. Würzburg, n. F.*, 35: 67–90.

——. 1905. Zellenstudien. V. Ueber die Abhängigkeit der Kerngrösse und Zellenzahl der Seeigel-Larven von der Chromosomenzahl der Ausgangszellen. *Jen. Z. Naturw.* 39 (n. F. 32): 445–524.

——. 1907. Zellenstudien. VI. Die Entwicklung dispermer Seeigeleier. Ein Beitrag zur Befruchtungslehre und zur Theorie des Kernes. *Jen. Z. Naturwiss.*, 43: 1–292.

——. 1914. *Zur Frage der Entstehung maligner Tumoren.* Jena.

Braungart, D. C., and G. E. Ott. 1942. A cytological study of the effect of colchicine on *Drosophila melanogaster*. *J. Hered.*, 33: 163–165.

Callan, H. G. 1941. A trisomic grasshopper. *J. Hered.*, 32: 296–298.

Carothers, E. E. 1941. Interspecific hybridization in the Acrididae (*Trimerotropis citrina* x *T. maritima*). *Genetics*, 26: 144.

Cockayne, E. A. 1938. The genetics of sex in Lepidoptera. *Biol. Rev.*, 13: 107–132.

Costello, D. P. 1942. Induced haploidy and triploidy in Californian *Triturus*. *Anat. Rec.*, 84, no. 4: 60.

Cowdry, E. V. 1943. Experimental epidermal methylcholanthrene carcinogenesis in mice. *Biol. Symposia*, 10: 131–162.

Crane, M. B., and S. S. Zilva. 1931. The antiscorbutic vitamin of apples. *J. Pomol. Hort. Sci.*, 9: 228–231.

Crecca, R. W., and S. L. Warner. 1944. The effects of methylcholanthrene on the integument of *Triturus viridescens*. Part II. Senior Thesis, Princeton University.

Crew, F. A. E. 1921. Sex-reversal in frogs and toads. A review of the recorded cases of abnormality of the reproductive system and an account of a breeding experiment. *J. Genet.*, 11: 141–181.

Cross, G. L., and T. J. Johnson. 1941. Structural features of the shoot apices of diploid and colchicine induced tetraploid strains of Vinca rosea. *Bull. Torrey Bot. Club*, 68: 618–635.

Dalcq, A. 1930. La formule chromosomiale chez la grenouille. *Ann. Bull. Soc. Roy. Sci. Med. nat. Bruxelles*, 1930: 15–21.

——. 1932. Contribution à l'analyse des fonctions nucléaires dans l'ontogénèse de la grenouille. IV. Modifications de la formule chromosomiale. *Arch. Biol. Paris*, 43: 343–366.

——, and S. Simon. 1931. Contribution à l'analyse des fonctions nucléaires dans l'ontogénèse de la grenouille. III. Etude statistique et cytologique des effets de l'irradiation d'un des gamètes sur la gastrulation chez *Rana fusca*. *Arch. Biol. Paris*, 42: 107–165.

Darlington, C. D., and K. Mather. 1944. Chromosome balance and interaction in *Hyacinthus*. *J. Genet*, 46· 52–61.

Dobzhansky, Th. 1929. The influence of the quantity and quality of chromosomal material on the size of the cells in *Drosophila melanogaster*. *Arch. EntwMech. Org.*, 115. 363–379.

Dodds, K. S. 1938. Chromosome numbers and spermatogenesis in some species of the hymenopterous family Cynipidae. *Genetica*, 20. 67–84.

Dooley, T. P. 1941. The influence of colchicine upon the germ cells of insects (Orthoptera) with special reference to the mitochondria and dictyosomes. *Trans. Amer. Micr. Soc.*, 60: 105–119.

Eigsti, O. J. 1942. A comparative study of mitosis in diploid and tetraploid species. *Amer. J. Bot.*, 29: suppl., 7.

Einset, J. 1942. Chromosome length in relation to transmission frequency of maize trisomics. *Genetics*, 28: 349–364.

——. 1944a. The occurrence of a tetraploid and two triploid apple seedlings in progenies of diploid parents. *Science*, 99: 345.

——. 1944b. Personal communication.

Erdman, L. H., and J. S. Thompson. 1943. Induction of triploidy in *Triturus viridescens* by heat-treatments. Senior Thesis, Princeton University.

Fabergé, A. C. 1936. The physiological consequences of polyploidy. I. Growth and size in the tomato. *J. Genet.*, 33: 365–382.

Fankhauser, G. 1925. Analyse der physiologischen Polyspermie des *Triton*-Eies auf Grund von Schnürungsexperimenten. *Arch. EntwMech. Org.*, 105: 501–580.

——. 1932a. Cytological studies on egg fragments of the salamander *Triton*. II. The history of the supernumerary sperm nuclei in normal fertilization and cleavage of fragments containing the egg nucleus. *J. Exp. Zool.*, 62: 185–235.

——. 1932b. The rôle of the chromosomes in the early development of merogonic embryos in *Triturus viridescens*. *Anat. Rec.*, 54, no. 3, suppl: 73.

——. 1934a. Cytological studies on egg fragments of the salamander *Triton*. III. The early development of the sperm-nuclei in egg fragments without the egg nucleus. *J. Exp. Zool.*, 67: 159–215.

——. 1934b. Idem. IV. The cleavage of egg fragments without the egg nucleus. *J. Exp. Zool.*, 67: 349–393.

——. 1934c. Idem. V. Chromosome number and chromosome individuality in the cleavage mitoses of merogonic fragments. *J. Exp. Zool.*, 68: 1–57.

——. 1937a. The production and development of haploid salamander larvae. *J. Hered.*, 28: 1–15.

——. 1937b. The development of fragments of the fertilized *Triton* egg with the egg nucleus alone ("gyno-merogony"). *J. Exp. Zool.*, 75: 413–469.

——. 1938a. The microscopical anatomy of metamorphosis in a haploid salamander, *Triton taeniatus* Laur. *J. Morph.*, 62: 393–413.

——. 1938b. Sex differentiation in a haploid salamander, *Triton taeniatus* Laur. *J. Exp Zool.*, 79: 35–49.

——. 1938c. Triploidy in the newt, *Triturus viridescens*. *Proc. Amer. Philos. Soc.*, 79: 715–739.

——. 1939. Polyploidy in the salamander, *Eurycea bislineata*. *J. Hered.*, 30: 379–388.

——. 1940a. Sex differentiation in triploid newts (*Triturus viridescens*). *Anat. Rec.*, 77: 227–245.

——. 1940b. A pentaploid larva of the newt, *Triturus viridescens*. *Proc. Nat. Acad. Sci., Wash.* 26: 526–532.

——. 1941a. Cell size, organ and body size in triploid newts (*Triturus viridescens*). *J. Morph.*, 68: 161–177.

——. 1941b. The frequency of polyploidy and other spontaneous aberrations of chromosome number among larvae of the newt, *Triturus viridescens*. *Proc. Nat. Acad. Sci. Wash.*, 27: 507–512.

——. 1942. Induction of polyploidy in animals by extremes of temperature. *Biol. Symposia*, 6: 21–35.

——, R. Crotta, and M. Perrot. 1942. Spontaneous and cold-induced triploidy in the Japanese newt, *Triturus pyrrhogaster*. *J. Exp. Zool.*, 89: 167–181.

——, and R. B. Griffiths. 1939. Induction of triploidy and haploidy in the newt, *Triturus viridescens*, by cold-treatment of unsegmented eggs. *Proc. Nat. Acad. Sci. Wash.*, 25: 233–238.

——, and R. R. Humphrey. 1942. Induction of triploidy and haploidy in axolotl eggs by cold treatment. *Biol. Bull.*, 83: 367–374.

——, and ——. 1943. The relation between number of nucleoli and number of chromosome sets in animal cells. *Proc. Nat. Acad. Sci. Wash.*, 29: 344–350.

——, and C. T. Kaylor. 1935. Chromosome numbers in androgenetic embryos of *Triturus viridescens*. *Anat. Rec.*, 64, no. 1, suppl. no. 1: 41–42.

——, and C. Moore. 1941a. Cytological and experimental studies of polyspermy in the newt *Triturus viridescens*. I. Normal fertilization. *J. Morph.*, 68: 347–385.

——, and ——. 1941b. Idem. II. The behavior of the sperm nuclei in androgenetic eggs (in the absence of the egg nucleus). *J. Morph.*, 68. 387–423.

——, and R. C. Watson. 1942. Heat-induced triploidy in the newt, *Triturus viridescens*. *Proc. Nat. Acad. Sci. Wash.*, 28: 436–440.

——, and ——. 1945. The effects of pituitary implants on diploid and triploid larvae of *Triturus viridescens* in premetamorphic stages. In press.

Flemming, W. 1879, 1880, 1882a. Beiträge zur Kenntnis der Zelle und ihrer Lebenserscheinungen. I, II, III. *Arch. mikr. Anat.*, 16: 302–436; 18: 151–259; 20: 1–86.

——. 1882b. *Zellsubstanz, Kern und Zelltheilung.* Leipzig.

Frolova, S. L. 1940. Cytology of development of parthenogenetic eggs of *Bombyx mori* L. activated by high temperature. *C. R. Acad. Sci. URSS*, 27: 604–606.

Giles, N. H. 1942. Autopolyploidy and geographical distribution in *Cuthbertia graminea* Small. *Amer. J. Bot.*, 29: 637–645.

Goldschmidt, R. 1931. Die sexuellen Zwischenstufen. *Berlin.*

——. 1937. Does the quantity of chromatin produce a genetic effect? *Amer. Nat.*, 71: 83–86.

——. 1938. *Physiological Genetics.* New York: McGraw-Hill.

Goodspeed, T. H., and P. Avery. 1939. Trisomic and other types in *Nicotiana sylvestris*. *J. Genet.*, 38: 381–458.

Gordon, M. 1945. The XY sex-chromosomes determine maleness in wild populations of *Platypoecilus maculatus* while the WZ determine femaleness in domesticated breeds of the same species. *Genetics*, 30: 6.

Greenleaf, W. H. 1938. Induction of polyploidy in *Nicotiana* by hetero-auxin treatment. *J. Hered.*, 29: 451–464.

Gremillion, D. F. 1942. Polyploidy in the germinal tissue of *Melanoplus femur-rubrum* (De G.). *Proc. Louisiana Acad. Sci.*, 7: 80–81.

Griffiths, R. B. 1941. Triploidy (and haploidy) in the newt, *Triturus viridescens*, induced by refrigeration of fertilized eggs. *Genetics*, 26: 69–88.

Gross, F. 1932. Untersuchungen über die Polyploidie und die Variabilität bei *Artemia salina*. *Naturwiss.*, 20: 962–967.

——. 1935. Die Reifungs- und Furchungsteilungen von *Artemia salina* im Zusammenhang mit dem Problem des Kernteilungsmechanismus. *Z. Zellforsch.*, 23: 522–565.

Gustafson, F. G. 1944. Growth hormone studies of some diploid and autotetraploid plants. *J. Hered.*, 35. 269–272.

Hadorn, E. 1932. Ueber Organentwicklung und histologische Differenzierung in transplantierten merogonischen Bastardgeweben. *Arch. Entw-Mech. Org*, 125· 495–565

——. 1934. Ueber die Entwicklungsleistungen bastard-merogonischer Gewebe von *Triton palmatus* (♀) x *Triton cristatus* ♂ im Ganzkeim und als Explantat in vitro. *Arch EntwMech. Org.*, 131: 238–284.

——. 1935. Chimärische *Triton*larven mit bastardmerogonischen und normalkernigen Teilstücken. *Rev Suisse Zool.*, 42: 417–426.

——. 1936. Uebertragung von Artmerkmalen durch das entkernte Eiplasma beim merogonischen *Triton*bastard, *palmatus* Plasma x *cristatus* Kern. *Verh. dtsch. zool. Ges., Freiburg*, 97–104.

——. 1937. Die entwicklungsphysiologische Auswirkung der disharmonischen Kern-Plasmakombination beim Bastard-merogon *Triton palmatus* (♀) x *Triton cristatus* ♂. *Arch. EntwMech. Org.*, 136: 400–489.

Hasimoto, H. 1933. Genetical studies on the tetraploid female in the silkworm. *Bull. Imp. Sericult. Exp. Sta.*, 8: 359–381.

——. 1934. Id. II. Occurrence of tetraploid female in a gynandromorphous strain. *Bull. Imp. Sericult. Exp. Sta.*, 8: 505–514.

Herlant, M. 1911. Recherches sur les oeufs di- et trispermiques de grenouille. *Arch. Biol. Paris*, 26: 103–335.

Herre, W. 1935. Hypophysenimplantationen bei Marmormolchlarven. *Verh. dtsch. zool. Ges.*, 37: 65–75.

——, and F. Rawiel. 1939. Implantation zusätzlicher Hypophysen in Larven verschiedener Molcharten. I. Die Wirkung auf die Geschlechtsorgane. *Arch. EntwMech. Org.*, 139: 86–109.

Hertwig, G. 1913. Parthenogenesis bei Wirbeltieren, hervorgerufen durch artfremden, radiumbestrahlten Samen. *Arch. mikr. Anat.*, 81, II: 87–127.

——. 1918. Kreuzungsversuche an Amphibien. I. Wahre und falsche Bastarde. *Arch. mikr. Anat.*, 91: 203–271.

——. 1927. Beiträge zum Determinations- und Regenerationsproblem mittels der Transplantation haploidkerniger Zellen. *Arch. EntwMech. Org.*, 111: 292–316.

——, and P. Hertwig. 1920. Triploide Froschlarven. *Arch. mikr. Anat.*, 94: 34–54.

Hertwig, O. 1913. Versuche an *Triton*eiern über die Einwirkung bestrahlter Samenfaden auf die tierische Entwicklung. *Arch. mikr. Anat.*, 82, II: 1–63.

Hertwig, P. 1916. Durch Radiumbestrahlung verursachte Entwicklung von halbkernigen *Triton*- und Fischembryonen. *Arch. mikr. Anat.*, 87, II: 63–122.

——. 1922. Bastardierung und Entwicklung von Amphibieneiern ohne mütterliches Kernmaterial. *Z. ind. Abst. Vererb.*, 27: 255–257.

——. 1923. Bastardierungsversuche mit entkernten Amphibieneiern. *Arch. EntwMech. Org.*, 100: 41–60.

Hilton, J. G. 1942. The effects of methylcholanthrene on the integument of Triturus viridescens. Senior Thesis, Princeton University.

Hiraiwa, Y. K, and T. Kawamura. 1936. Relation between maturation division and cleavage in artificially activated eggs of *Urechis unicinctus* (von Drasche). *Biol. Bull*, 70: 344–351.

Hirobe, T. 1939. Polyploid silkworm induced by colchicine treatment upon eggs. *Jap. J. Genet.*, 15: 69–74.

Hoerstadius, S., and A. Wolsky. 1936. Studien über die Determination der Bilateralsymmetrie des jungen Seeigelkeimes. *Arch. EntwMech. Org.*, 135: 69–113

Holtfreter, J. 1943. Properties and functions of the surface coat in amphibian embryos. *J. Exp. Zool.*, 93· 251–323.

Hovasse, R. 1922 Contribution à l'étude des chromosomes. Variations du nombre et régulation en parthénogénèse. *Bull. biol. France et Belg.*, 56: 141–229.

Humphrey, R. R. 1942a. Sex of the offspring fathered by two *Amblystoma* females experimentally converted into males. *Anat. Rec.*, 82, no. 3: 77.

Humphrey, R. R. 1942b. Sex reversal and the genetics of sex determination in the axolotl (*Amblystoma mexicanum*). *Anat. Rec.*, 84, no. 4: 15.

——. 1945. Sex determination in ambystomid salamanders: a study of the progeny of females experimentally converted into males. *Amer. J. Anat.*, 76: 33–66.

——, and G. Fankhauser. 1943. Two unusual haploid-diploid mosaics of mixed *Amblystoma* *mexicanum* and *Amblystoma tigrinum* ancestry. *Anat. Rec.*, 87, no. 4: 23.

Husted, L. 1943. Personal communcation.

Inaba, F. 1939. Polyploidy in *Habrobracon* induced by colchicine treatment. (A preliminary note). *Jap. J. Genet.*, 15: 344–347.

——. 1940. Polyploidy in *Habrobracon* induced by colchicine treatment. II. Production of impaternate females. *Jap. J. Genet.*, 16: 270–272.

Kawaguchi, E. 1936. Der Einfluss der Eierbehandlung mit Zentrifugierung auf die Vererbung bei dem Seidenspinner. I. Ueber experimentelle Auslösung der polyploiden Mutation. *J. Fac. Agric.* (*Sapporo*), 38: 111–133.

Kawamura, T. 1939a. Artificial parthenogenesis in the frog. I. Chromosome numbers and their relation, to cleavage histories. *J. Sci. Hirosima Univ., Ser. B, Div.* 1, 6: 115–218.

——. 1939b. Id. II. The sex of parthenogenetic frogs. *J. Sci. Hirosima Univ., Ser. B, Div. 1*, 7: 39–86.

——. 1940. Id. III. The development of the gonads in triploid frogs and tadpoles. *J. Sci. Hirosima Univ., Ser. B, Div. 1*, 8: 117–164.

Kaylor, C. T. 1937. Experiments on androgenesis in the newt, *Triturus viridescens*. *J. Exp. Zool.*, 76: 375–394.

——. 1940a. Studies on experimental haploidy in salamander larvae. I. Experiments with eggs of the newt, *Triturus pyrrhogaster*. *Biol. Bull.*, 79: 397–408.

——, 1940b. Experiments on the parabiotic union of haploid and diploid larvae of *Triturus pyrrhogaster*. *Anat. Rec.*, 78, no. 4, suppl.: 52–53.

——. 1941. Studies on experimental haploidy in salamander larvae. II. Cytological studies on androgenetic eggs of *Triturus viridescens*. *Biol. Bull.*, 81: 402–419.

——. 1943. Sex differentiation in two androgenetic salamander larvae, *Triturus pyrrhogaster*. *Anat. Rec.*, 87: 127–139.

Keppel, D. M., and A. B. Dawson. 1939. Effects of colchicine on the cleavage of the frog's egg (*Rana pipiens*). *Biol. Bull.*, 76: 153–161.

King, R. L., and E. H. Slifer. 1934. Insect development. VIII. Maturation and early development of unfertilized grasshopper eggs. *J. Morph.*, 56: 603–619.

Knapp, E. 1939. Haploide Pflanzen von *Antirrhinum majus*. *Ber. dtsch. bot. Ges.*, 57: 371–379.

Kostoff, D. 1938. Directed hereditable variations conditioned by euploid chromosome alterations in higher plants. *Nature Lond.*, 142: 1117.

——, and I. A. Axamitnaja. 1935. Studies on polyploid plants. IX. Chemical analysis of diploid and their autotetraploid plants. *C. R. Acad. Sci. URSS*, 2, no. 34: 293–297.

Lehmann, F. E., and H. Woker. 1940. Verschwinden embryonaler Zellkerne von *Tubifex* nach Colchicinbehandlung. *Verh. Schweiz. Naturf. Ges., Locarno:* 181–182.

Lesley, J. W. 1928. A cytological and genetical study of progenies of triploid tomatoes. *Genetics*, 13: 1–43.

Lesley, M. M., and J. W. Lesley. 1930. The mode of origin and chromosome behaviour in pollen mother cells of a tetraploid seedling tomato. *J. Genet.*, 22: 419–425.

Levy, F. 1920a. Ueber die sogenannten Ureier im Froschhoden. *Biol. Zbl.*, 40: 29–37.

——. 1920b. Die Kernverhältnisse bei parthenogenetischen Fröschen. *Sitzber. Preuss. Akad. Wiss.*, 24: 417–425.

Li, Ju-Chi. 1927. The effect of chromosomal aberrations on development in *Drosophila melanogaster*. *Genetics*, 12· 1–58.

Michalski, J. V. 1942. Spontaneous aberrations in chromosome number (triploidy and haploidy) among larvae of the two-lined salamander, *Eurycea bislineata*. Ph.D. Thesis, Princeton University.

Mickey, G. H. 1942a. Polysomaty and polyploid gametes in *Romalea microptera*. *Genetics*, 27: 156.

——. 1942b. Polyploid gametes in the Louisiana lubber grasshopper. *Proc. Louisiana Acad. Sci.*, 6: 82.

de Mol, W. E. 1921. De l'existence de variétés hétéroploides de l'*Hyacinthus orientalis* L. dans les cultures hollandaises. *Arch. néerl. Sci. III B*, 4: 18–117.

Morgan, T. H. 1927. *Experimental Embryology.* New York: Columbia Univ. Press.

——, C. B. Bridges, and A. H. Sturtevant. 1925. The genetics of *Drosophila*. *Bibl. Genet.*, 2: 1–262

Müntzing, A. 1941. New material and cross combinations in *Galeopsis* after colchicine-induced chromosome doubling. *Hereditas*, 27: 193–201.

Naguti, Y., K. Okuma, and H. Oka. 1939. Studies on the polyploidy in *Nicotiana* induced by the treatment with colchicine. I. General observations on the autotetraploid of *N. rustica* and *N. tabacum*. *Jap. J. Bot.*, 10: 309–319.

Navashin, M. 1925. Polyploid mutations in *Crepis*. Triploid and pentaploid mutants of *Crepis capillaris*. *Genetics*, 10: 583–592.

Needham, J. 1936. New advances in the chemistry and biology of organized growth. *Proc. Roy. Soc Med.*, 29: 1577–1626.

——. 1942. *Biochemistry and Morphogenesis.* Cambridge: Cambridge Univ. Press.

Nilsson-Ehle, H. 1936. Ueber eine in der Natur gefundene Gigasform von Populus tremula. *Hereditas*, 21: 379–382.

Oehninger, M. 1913. Ueber Kerngrössen bei Bienen. *Verh. phys.-med. Ges. Würzburg*, 42: 135–140.

O'Mara, J. G. 1942. A photoperiodism accompanying autotetraploidy. *Amer. Nat.*, 76: 386–393.

Painter, T. S. 1923. Studies in mammalian spermatogenesis. II. The spermatogenesis of man. *J. Exp. Zool.*, 37: 291–336.

Parmenter, C. L. 1933. Haploid, diploid, triploid, and tetraploid chromosome numbers and their origin in parthenogenetically developed larvae and frogs of *Rana pipiens* and *Rana palustris*. *J. Exp. Zool.*, 66: 409–453.

——. 1940. Chromosome numbers in *Rana fusca* parthenogenetically developed from eggs with known polar body and cleavage history. *J. Morph.*, 66: 241-260.

Pincus, G., and H. Shapiro. 1940. Further studies on the parthenogenetic activation of rabbit eggs. *Proc. Nat. Acad. Sci. Wash.*, 26: 163–165.

——, and C. H. Waddington. 1939. The effect of mitosis-inhibiting treatments on normally fertilized pre-cleavage rabbit eggs. *J. Hered.*, 30: 515–518.

Ponse, K. 1930. Le problème du sexe et l'évolution de l'organe de Bidder du crapaud. *Proc. 2nd Intern. Congr. Sex Res. Edinb.* · 202–210.

——. 1941. La proportion sexuelle dans la descendance issue des oeufs produits par l'organe de Bidder de crapauds femelles. (Note préliminaire). *Rev. Suisse Zool.*, 48: 541–544.

Porter, K. R. 1939 Androgenetic development of the egg of *Rana pipiens*. *Biol. Bull.*, 77: 233–257.

Randolph, L. F. 1941. Personal communication.

——. 1942. The influence of heterozygosis on fertility and vigor in autotetraploid maize. *Genetics* 27: 163.

——, E. C. Abbe, and J. Einset. 1944. Comparison of shoot apex and leaf development in diploid and tetraploid maize. *J. Agric. Res.*, 69: 47–76.

——, and H. E. Fischer. 1939. The occurrence of parthenogenetic diploids in tetraploid maize. *Proc. Nat. Acad. Sci. Wash.*, 25: 161–164.

——, and D. B. Hand. 1938. Increase in vitamin A activity of corn caused by doubling the number of chromosomes. *Science*, 87: 442–443.

——. 1940. Relation between carotenoid content and number of genes per cell in diploid and tetraploid corn. *J. Agric. Res.*, 60: 51–64.

Retzius, G. 1881. Studien über die Zellentheilung. *Biol. Untersuch.*, 1881: 109–134.

Rhoades, M. M. 1936. Note on the origin of triploidy in maize. *J. Genet.*, 33: 355–357.

Risman, G. C. 1942. Cell size in Habrobracon. *Genetics*, 27: 166.

Robbins, W. J., and V. Kavanach. 1943. Growth of excised roots of polyploid tomatoes. *Amer. J. Bot.*, 30: 602–605.

Rostand, J. 1933. Influence du refroidissement sur le développement des oeufs hybrides *Bufo* ♀ x *Rana* ♂. *C. R. Soc. Biol. Paris*, 113: 346–347.

——. 1934. Gynogenèse du crapaud par refroidissement de l'oeuf. *C. R. Soc. Biol. Paris*, 115: 1680–1681.

——. 1936. Gynogenèse par refroidissement des oeufs chez Hyla arborea. *C. R. Soc. Biol. Paris*, 122: 1012–1013.

——. 1938. La parthénogenèse des vertébrés. *Act. Sci. Industr.*, no. 651. *Paris.*

Rotmann, E. 1940. Die Bedeutung der Zellgrösse für die Entwicklung der Amphibienlinse. *Arch. EntwMech. Org.*, 140: 124–156.

Rugh, R. 1939. Developmental effects resulting from exposure to X-rays. *Proc. Amer. Philos. Soc.*, 81: 447–471.

——, and D. A. Marsland. 1943. The effect of hydrostatic pressure upon early development of the frog's egg (*Rana pipiens*). I. Macroscopic observations. *Proc. Amer. Philos. Soc.*, 86: 459–466.

Sansome, F. W., and S. S. Zilva. 1933. Polyploidy and vitamin C. *Biochem. J.*, 27: 1935–1941.

Satina, S., A. F. Blakeslee, and A. G. Avery. 1937. Balanced and unbalanced haploids in *Datura*. *J. Hered.*, 28: 192–202.

Seiler, J. 1927. Ergebnisse aus der Kreuzung parthenogenetischer und zweigeschlechtlicher Schmetterlinge. *Biol. Zbl.*, 47: 426–446.

——. 1936. Neue Ergebnisse aus der Kreuzung parthenogenetischer Schmetterlinge mit Männchen zweigeschlechtlicher Rassen. *Verh. dtsch. zool. Ges.*, 147–150.

——. 1937. Ergebnisse aus der Kreuzung parthenogenetischer und zweigeschlechtlicher Schmetterlinge. V Die *Solenobia*-Intersexe und die Deutungen des Phanomens der Intersexualität. *Rev. Suisse Zool.*, 44: 283–307.

Shifriss, O. 1942. Polyploids in the genus *Cucumis*. *J. Hered*, 33: 144–152.

Shkvarnikov, P. K. 1934. Ueber den Einfluss einzelner Chromosomen auf die Grosse der Zellen. *Biol. Zh.*, 3. 533–545.

Shull, G. H. 1929. An unexpected association of factors belonging to three linkage groups of *Oenothera* and its explanation. *Proc. Nat. Acad. Sci. Wash.*, 15: 268–274.

Sinnott, E. W., and A. F. Blakeslee. 1938. Changes in shape accompanying tetraploidy in cucurbit fruits. *Science*, 88: 476.

——, and A. H. Franklin. 1943. A developmental analysis of the fruit in tetraploid as compared with diploid races of cucurbits. *Amer. J. Bot.*, 30: 87–94.

——, and V. V. Trombetta. 1936. The cytonuclear ratio in plant cells. *Amer. J. Bot.*, 23: 602–606.

Smith, H. E. 1943. Polyploidy in *Sedum pulchellum*. II. Stomatal size and frequency. *Bull. Torrey Bot. Club*, 70: 261–264.

SMITH, H. H. 1943. Studies on induced heteroploids of *Nicotiana*. *Amer. J. Bot*, 30: 121–130.

SMITH, L. 1942. Cytogenetics of a factor for multiploid sporocytes in barley. *Amer. J. Bot.*, 29: 451–455.

SPEICHER, B. R. 1935. Cell size and chromosomal types in *Habrobracon*. *Amer. Nat.*, 69: 79–80.

——, and L. G. SPEICHER. 1940. The occurrence of diploid males in *Habrobracon brevicornis*. *Amer. Nat.*, 74: 379–382.

SPEMANN, H. 1914. Ueber verzögerte Kernversorgung von Keimteilen. *Verh. dtsch. zool. Ges.*, *24. Jahresvers.*, *Freiburg i. Br:* 216–221.

——, and H. FALKENBERG. 1919. Ueber asymmetrische Entwicklung und Situs inversus viscerum bei Zwillingen und Doppelbildungen. *Arch. Entw-Mech. Org.*, 45: 371–422.

STALKER, H. D. 1942. Triploid intersexuality in *Drosophila americana* Spencer. *Genetics*, 27: 504–518.

STOUT, A. B., and C. CHANDLER. 1941. Change from self-incompatibility to self-compatibility accompanying change from diploidy to tetraploidy. *Science*, 94: 118.

STRAUB, J. 1940. Quantitative and qualitative Verschiedenheiten innerhalb von polyploiden Pflanzenreihen. *Biol. Zbl.*, 60: 659–669.

SULKIN, N. M. 1943. A study of the nucleus in the normal and hyperplastic liver of the rat. *Amer. J. Anat.*, 73: 107–125.

TÄCKHOLM, G. 1922. Zytologische Studien über die Gattung *Rosa*. *Acta Hort. Berg.*, 7: 97–381.

TAYLOR, J. H. 1942. A physiological study of diploid and related tetraploid plants. *Proc. Okla. Acad. Sci.*, 22: 137–138.

TCHOU-SU. 1931. Etude cytologique sur l'hybridation chez les anoures. *Arch. Anat. micr.*, 27: 1–105.

——. 1936. L'hybridation chez les anoures de Canton (Chine). *C. R. Acad. Sci. Paris*, 202: 242–244.

TORVIK, M. M. 1931. Genetic evidence for diploidism of biparental males in *Habrobracon*. *Biol. Bull.*, 61: 139–156.

TROMBETTA, V. V. 1942. The cytonuclear ratio. *Bot. Rev.*, 8: 317–336.

TYLER, A. 1941. Artificial parthenogenesis. *Biol. Rev.*, 16: 291–336.

VANDEL, A. 1927. Gigantisme et triploidie chez l'isopode *Trichoniscus* (*Spiloniscus*) *provisorius* Racovitza. *C. R. Soc. Biol. Paris*, 97: 106–108.

——. 1928. La parthénogenèse géographique. *Bull. Biol. France Belg.*, 62: 164–281.

——. 1934. Id. II. Les mâles triploides d'origine parthénogénétique de *Trichoniscus* (*Spiloniscus*) *elisabethae* Herold. *Bull. Biol. France Belg.*, 68: 419–463.

WADDINGTON, C. H. 1935. Cancer and the theory of organizers. *Nature*, 135: 606–608.

WAGNER, C. E. 1944. Experiments on artificial parthenogenesis of eggs of the newt *Triturus viridescens*. Senior Thesis, Princeton University.

WARMKE, H. E., and A. F. BLAKESLEE. 1939. Induction of simple and multiple polyploidy in *Nicotiana* by colchicine treatment. *J. Hered.*, 30: 419–432.

VON WETTSTEIN, F. 1937. Experimentelle Untersuchungen zum Artbildungsproblem. I. Zellgrössenregulation und Fertilwerden einer polyploiden *Bryum*-Sippe. *Z. ind. Abst. Vererb.*, 74: 34–53.

——. 1940. Idem. II. Zur Frage der Polyploidie als Artbildungsfaktor. *Ber. dtsch. bot Ges.*, 58: 374–388.

WHITING, A. R. 1928. Genetic evidence for diploid males in *Habrobracon*. *Biol. Bull.*, 53: 438–449.

WINKLER, H. 1916. Ueber die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. *Z. Bot.*, 8. 417–531

WITSCHI, E. 1923. Ueber die genetische Konstitution der Froschzwitter. *Biol. Zbl.*, 43. 83–96.

——. 1929. Studies on sex differentiation and sex determination in amphibians. III. Rudimentary hermaphroditism and Y chromosome in *Rana temporaria*. *J. Exp. Zool.*, 54: 157–223.

——. 1934. Genes and inductors of sex differentiation in amphibians. *Biol. Rev.*, 9: 460–488.

WOKER, H. 1943. Phasenspezifische Wirkung des Colchicins auf die ersten Furchungsteilungen von *Tubifex*. *Rev. Suisse Zool.*, 50: 237–243.

——. 1944. Die Wirkung des Colchicins auf Furchungsmitosen und Entwicklungsleistungen des *Tubifex-Eies*. *Rev. Suisse Zool.*, 51: 109–171.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

GENERAL BIOLOGY

GENERATION OF ANIMALS. *Loeb Classical Library. By Aristotle. Translated by A. L. Peck. Harvard University Press, Cambridge, Mass.; Wm. Heinemann, London.* $2.50 (cloth); $3.50 (leather). lxxviii + 608 pp. 1943.

This is indeed a welcome addition to the Loeb Classical Library, for the *De Generatione Animalium* has been strangely neglected by translators in comparison with the *Historia Animalium*. The only recent translation into English of the former treatise, that made by Arthur Platt in 1910, can hardly bear contrast with D'Arcy Thompson's masterly translation of the *Historia*. It is rare indeed that so happy a combination of classical scholarship and biological knowledge as Thompson's can be found to undertake the translation of the great biological works of antiquity. Dr Peck, of Christ's College, Cambridge, makes no claim to a professional knowledge of biology, but it is evident, from his preface and footnotes, that he has profited much by discussion with Joseph Needham and other biologists of his university. That he is himself a classical scholar of discernment is equally apparent in the excellent introduction, in which Aristotle's natural philosophy of causes is discussed, along with the varied meanings to be given to such key words as *Logos*, *Arche*, *Physis*, *Dynamis*, *Pneuma*, and *Psyche*; in the description and evaluation of the MS sources and emendations; in the footnotes and appendices, which serve admirably to clarify Aristotle's views; and, most important of all, in the translation itself, which achieves notable clarity and distinction in the use of the English in place of the Greek idiom. The translator has also avoided the pitfall of translating Aristotle's technical terms by those of modern biology so as to render the treatise pseudo-modern in style. A slip is the translation of *tetrapodon* as "fishes" (754a17); while the translation of *myria* as "heaps of others" is schoolboy slang; but these are rare and minor imperfections. There is a full outline of the contents of the treatise, and an index. As in all volumes of this series, Greek text and translation face one another.

As to the work itself, it might well take its place alongside the *Historia Animalium* in Raymond Pearl's *To Begin With* as required reading for all young biologists. In fact, of the two, the *Generation of Animals* is probably the more important, since here, as Dr. Peck has justly remarked, "Aristotle's thought is to be seen integrated as it is nowhere else; for in reproduction, as understood by Aristotle, not only the individual is concerned but the cosmos at large." The student should read it also for the numerous observations bearing on animal reproduction, heredity, and embryology, many of them amazingly accurate, many others erroneous or incomplete—one wonders, for example, whether Aristotle can ever have really seen insects in copulation. The student should also read it for the relation of fact to theory, as it is here that Aristotle achieved his most astonishing successes and made his most egregious blunders. His discernment of the epigenetic nature of development and the action of "principles" resembling hormones and morphogenetic movements in development was the product of the same logical processes of induction and deduction that led him to regard the determination of sex as due to the success or failure of the male "principle" in the semen to gain the mastery over the material (menstrual fluid) provided by the female, since the latter substance, if properly concocted, would develop into a male, but, with a deficiency of heat, would change over into the opposite condition and become female.

The wealth of material in the treatise is fascinating and well-nigh inexhaustible, and he who reads will find many a suggestion for experiment and observation even today. *Peri Zoion Geneseon* is no longer the Bible of biology, but it is indeed its genesis.

BENTLEY GLASS

THE RELIGIOUS AND PHILOSOPHICAL ASPECTS OF VAN HELMONT'S SCIENCE AND MEDICINE. *Supplement to the Bulletin of the History of Medicine, No. 2.*

By Walter Pagel. The Johns Hopkins Press, Baltimore. $1.00 (paper). ix + 44 pp. 1944.

Textbooks in the history of medicine, biology, and chemistry list a great number of fundamental scientific discoveries (introduction of the concept of gas, important insight into fermentation, digestion, metabolism, etc.) due to van Helmont (1577-1644) and omit a few more. The general opinion is that van Helmont made these discoveries in spite of his "queer" religious and philosophical opinions. Pagel has consistently opposed this psychologically and historically equally unfounded assumption since 1930, and he has shown that "van Helmont's biological bent is due to his religious zeal, and his scientific achievement the fruit of his religious conviction." "Religious motives led van Helmont (a) to scepticism towards human reason and (b) to empiricism as the way of truth and reality." As Pagel's earlier work is mostly written in German, it is most welcome to have now a short summary of his findings in English. This work has a larger significance than that of merely correcting errors concerning the individual scientist van Helmont, with whom the present small treatise deals perhaps too exclusively. It largely contributes to a better understanding of seventeenth century science and scientists in general. During the last fifteen years, we have learned (or relearned) that the primary motives of almost all great seventeenth century scientists were religious ones, and we will now have to look rather for those rare seventeenth century scientists who may have acted independently of such religious motivations.

To most biologists without historical training the book of Pagel will probably come as rather a shock. But it is perhaps not useless for them to learn that in scientific work, also, many ways may lead to the "Rome" of discovery and insight, and that after all the actual progress of scientific thought is a much more complicated thing than we are inclined to think on the basis of our own candor and the nice fables we are told in our youth.

ERWIN H. ACKERKNECHT

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THE WOODS HOLE MARINE BIOLOGICAL LABORATORY.

By Frank R. Lillie. University of Chicago Press, Chicago. $4.00. ix + 284 pp. 1944.

Many histories could and doubtless will be written about Woods Hole and its laboratories. Among them this volume will always occupy a special place because it alone is, as far as possible, an eyewitness account put on paper, "Before all those concerned with the early development of the Marine Biological Laboratory are gone . . . and it becomes too late to recapture the early enthusiasm that went into its making." The writing of this well illustrated, well printed, and well documented book by Frank Lillie (and E. G. Conklin, who collaborated generally and wrote certain sections) must have been a labor, but a labor of love.

These authors have succeeded in recapturing much of the "Woods Hole spirit," but they have done a great deal more. They have presented a highly informative and systematic account of the life history of a laboratory that is unique among institutions of its size and importance in being wholly controlled—peopled, administered, "trusteed"—by the scientific investigators who use it, and unique also in the extent of the role it has played in the development of biological research throughout the United States. The scope of this history extends from a time before Woods Hole was a a whaling port down to the 1940's.

Here the reader will discover many unfamiliar and sometimes curious facts about the founding and early activities of marine biological laboratories in both Europe and America. Here also he will find a photograph of the justly famous motto of the Penikese laboratory in Louis Agassiz's elegant copybook calligraphy, "Study nature not books," and the familiar picture of Agassiz lecturing at Penikese beside a blackboard covered with his diagrams of Radiates. The following pages describe the material and scientific growth of the Woods Hole Laboratory. Perhaps the most interesting feature is a series of eleven thumbnail sketches drawn around problems that formed centers of activity during the first twenty years. Including the investigators involved, it makes impressive reading: Animal Morphology, Descriptive Embryology, Experimental Embryology, Regeneration, Fertilization and Parthenogenesis, Cytology, Genetics and Evolution, General Physiology, Animal Tropisms and Behavior, Botany, the Medical Sciences. This parade is followed by a chapter portraying four early leaders, including Charles O. Whitman and Charles R. Crane.

The book ends with a sufficiently broad account of the social life of Woods Hole, the work and organization of the Woods Hole Oceanographic Institution, and finally an appendix of some seventy-six pages. Even in this last forbidding section the veriest outsider will find much that is rewarding imbedded in a frankly tedious matrix of committee reports, formal resolutions, and acts of incorporation. For it is there that he may see many of the actual wheels and cogs by which the laboratory has moved. The present generation of biologists may take heart from these fossil records of "battles long ago" that some supposed were but the inevitable death struggles of a laboratory run entirely by biologists.

This volume should have a useful function in interpreting the Woods Hole laboratories to the educated public. We know of few comparable books in which it is made as clear as it is here that scientific research depends for its ultimate support on an enlightened public.

G. B. MOMENT

A SOURCE OF BIOLOGICAL NAMES AND TERMS.

By Edmund C. Jaeger. Charles C. Thomas, Springfield and Baltimore. $3.50. xxvi + 256 pp. 1944.

This book is a carefully compiled, thorough, and easy-to-use guide to the etymology of technical terms in biology. It is essentially an alphabetical list of the stems or elements from which biological names and descriptive terms are compounded. Each stem is first cited; then the corresponding Greek, Latin, or modern word from which its use is derived; next the meaning or meanings; and finally, as examples, a number of technical words in which the stem appears, chosen to illustrate the various forms taken by the combining elements. By this arrangement the derivation and meaning of scientific terms are easily looked up and understood. A number of clear pen drawings lighten the appearance of the pages and serve to illustrate some of the characteristics and the resemblances, obvious or fanciful, upon which biologists have based their coinage of names. The list is said to contain 12,000 word-elements and to exceed by manyfold the scope of the unabridged dictionaries. Check of a few pages against one of the dictionaries fully corroborates this claim. Such a list cannot, of course, always explain a word fully without the parallel use of a dictionary. The choice both of terms listed and of examples refers primarily to descriptive zoölogy and botany, but many terms of mammalian anatomy, physiology, and medicine are included. In an excellent introduction, based in part on the preface of J. S. Palmer's *Index Generum Mammalium*, the author expounds the principles of scientific word-compounding and points out some of its puzzles and pitfalls.

Jaeger, who is a naturalist by profession, has based his philological work upon reliable sources and has obviously taken great pains to insure accuracy. The reviewer, after careful study, has noticed only one error, namely that under the stem *Trochant—* the anatomical term "trochanter" is wrongly defined, and the only cited meaning of the Greek word "*trochanter*" ("runner") is probably not quite relevant, for Josef Hyrtl, a great authority on such matters, thought that the process of the mammalian femur known by this term was named from a secondary use of the Greek word to designate the tiller of a boat. What few errors may be present in Jaeger's book are probably in special fields like this.

The book will be very useful to experienced biological writers and teachers; and for students it should be invaluable. Those who have a feeling for words and have studied classical languages will enjoy its use; those to whom etymology and terminology are obscure, burdensome, or vexatious matters will find in these pages a convenient source of help.

GEORGE W. CORNER

MAN AND HIS BIOLOGICAL WORLD.

By Frank Covert Jean, Ezra Clarence Harrah, and Fred Louis Herman, with the editorial collaboration of Samuel Ralph Powers. Ginn and Company, Boston. $3.50. viii + 631 pp. 1944.

This text for a college course in general biology is a revision of *Man and the Nature of His Biological World*, an earlier work by the same authors. The field surveyed is divided into nine units, dealing respectively with protoplasm and its metabolic activities; reproduction; nervous, hormonal, and other types of coordination and responsiveness; the nature and control of disease; the natural cycles; the balance of nature; evolution; genetics; and human cultural development. Most sections are clearly written, up to date, and errors are not numerous.

Exception must be taken, however, to the first chapter on genetic principles, which needs extensive revision and correction. The continuous spireme is still figured in mitosis; chromosome pairing in meiosis is said to take place as the chromosomes become arrayed at the equator of the spindle; the first meiotic division is described as purely reductional, the second as an ordinary mitosis; different symbols are used for alleles in discussing segregation and independent assortment in a highly confusing fashion; and there are numerous minor inaccuracies and unclear statements. The discussion of eugenic principles in a later chapter repeats some dubious conclusions. There is a tendency to preach: "Unworthy living, the excessive use of alcoholic liquors and drugs, or the contraction of venereal diseases on the part of the parents, may, through direct injury to the germ plasm, tragically blast and blight the health of the offspring throughout their whole lives." Perhaps the inheritance of acquired characteristics is not implied here, but freshmen will certainly be misled.

Another chapter that arouses criticism is the one on the present status of Darwinism. Natural selection is here treated in too narrow a sense. "For instance, it is maintained" by those criticizing the theory of natural selection "that many organisms have succeeded not so much by killing off less favorable variations as by possessing the characteristics that enabled them to succeed and multiply more abundantly in a given environment." The chapter then ends with a division of biologists into seemingly equal groups of those "who favor the purely selective position of Darwin and those who adhere to the idea of a more or less directed evolution." Authorities are arrayed on both sides, and the conclusion is reached, on the basis of Henry Fairfield Osborn's stand, that "we are more at a loss than ever before to understand the causes of evolution." In view of the availability of such excellent analyses of the causes of evolution as those by Dobzhansky, Haldane, and Julian Huxley, this is flatly antiquated.

Aside from these sections, the book may be recommended. Illustrations are abundant and well chosen, but not always clearly reproduced or provided with adequate legends. There are questions for study and a list of references after each chapter, and a glossary and index at the end of the book.

BENTLEY GLASS

PAPERS ON ARCHAEOLOGY, ECOLOGY, ETHNOLOGY, HISTORY, PALEONTOLOGY, PHYSICS, AND PHYSIOLOGY. *Proceedings of the American Philosophical Society, Volume 87, Number 5.*

Various Authors. The American Philosophical Society, Philadelphia. $1.00 (paper). Pp. 365–460. 1944.

This number contains twelve papers, five of them being on biological subjects. "The Correspondence between Constantine Samuel Rafinesque and Thomas Jefferson," by Edwin M. Betts, is valuable for the light it throws on Rafinesque's work while at Transylvania University, on his devotion to science, and on his unavailing efforts to be appointed a professor at the newly founded University of Virginia. "The Earliest Account of the Association of Human Artifacts with Fossil Mammals in North America," by M. F. Ashley Montagu and C. Bernard Peterson, resurveys the purported discoveries by Albert Koch in 1839 of human artifacts associated with the remains of fossil mastodons and ground sloths, and establishes the high probability that Koch indeed made a genuine discovery, including that of the first Folsom point. G. H. Parker discusses "The Time Factor in Chromatophore Responses," and points out that, when a broad survey is made of animals showing melanophore changes, the evidence shows that nervous control is not always more rapid than hormonal control in producing a response. The dependence of both types of control on the mechanism of neurohumors is indicated. P. Lecomte du Nouy considers "Physiological Time" in a brief summary of ideas developed at length in his book *Biological Time.* Although not new, this essay is a proper rebuke to those who carried on the prolonged discussion of biological time in the columns of *Science* in 1944 without troubling to inform themselves of standard work on the subject. The longest of the five biological articles is "Studies on the Army-Ant Behavior Pattern.—Nomadism in the Swarm-Raider *Eciton burchelli,*" by T. C. Schneirla. This is a full and very interesting account of the dependence of bivouac removal, in this species, on the development of intensive raiding during the day, on the decline of illumination in the afternoon, on traffic conditions, and on the "threshold of arousal" in the colony, but not on the scarcity or abundance of food in the vicinity of the community, as commonly supposed.

BENTLEY GLASS

STAIN TECHNIQUE.

By W. H. Emig. W. H. Emig, University of Pittsburgh. $1.00 (paper). 75 pp. 1941.

One can find in this handbook specific information about the properties and uses of 188 different biological stains, grouped under the headings of synthetic organic dyes (twenty-six classes), natural organic dyes, and inorganic coloring matters, and arranged in the order of their color index numbers. There are four brief general chapters. The second, on the chemical and physical properties of dyes, discusses color precipitates, reversible reactions, oxidations and reductions, and physical properties. The third, on the uses of stains, considers acid dyes, direct dyes, basic dyes, and dye nomenclature. The fourth discusses the principles of selecting contrasting stains for combinations. The whole manual represents an attempt to substitute a logical understanding of the uses of dyes, based upon their chemical and physical properties, for the pragmatic methods that at present so congest our handbooks and journals of microtechnique.

The discussions of the individual dyes give synonyms, type (acid, direct, basic, etc.), fastness to light, formula for solution, and some comments on uses in staining tissues, mainly those of plants. The chemical names and structures of the dyes, except in rare instances, are not given. That the handbook is not always accurate nor up to date is shown by the fact that it lists Janus green B, so useful in supravital staining, as obsolete; orcein, widely used for the giant dipteran salivary chromosomes and for elastic fibers, as principally an indicator; and basic fuchsin, used in Feulgen's specific stains for nucleic acid and glycogen, only as a stain for bacteria and vascular plant tissues. In spite of such faults and the inadequate basis at the present time for a complete treatment of the projected type, there is no doubt that this handbook will prove very useful.

ECOLOGY

UNBIDDEN HOUSE GUESTS.

By Hugo Hartnack. Hartnack Publishing Company, Tacoma. $12.00. 560 pp. 1943.

One is greatly impressed with the original manner in which this book has been written and compiled. It is not a textbook, yet it contains a world of factual information; it is not a novel, yet it holds one's interest and supplies genuine amusement. The author has apparently made every effort to enliven a subject that otherwise might prove boring to many. He has included interesting historical sidelights wherever possible and has dotted the pages with humorous cartoons that may or may not relate directly to the text material. The book covers a tremendous field, as evidenced by the fact that this is only the first of two volumes to be published. "An unbidden house guest" is considered to be any undesirable plant or animal that ventures on or within a dwelling. The scope of the material is still broader, since some of these house pests bring with them other plants and animals that cause human disease. To be a bit facetious, in view of the completeness of the book, one cannot help but wonder if the author will discuss in his second volume how to rid the house of other specimens of *Homo sapiens* who are no longer welcome.

The author came to the United.States from Germany in 1924. From his experience as a pest control operator, he has observed a need here in America for a book informing various groups about the habits of pests and the ways of controlling them. Although his background has made it practically impossible to eliminate all Germanisms from his style, it has made it possible for him to furnish his English readers with valuable information obtained from the literature of his native country. Apparently this extensive source of information has been largely overlooked by workers in this country. The freshness of his book is due to a great extent to the reproductions of many excellent illustrations from European publications.

After a lengthy introductory section, he takes up the plant and animal kingdoms in an orderly manner and discusses the pests, parasites, and micro-organisms that belong to each of the major phyla, classes, and orders. The one notable omission is that of the true insects, which are to be presented in the second volume.

It is unfortunate that the sale of this book has been restricted to 1500 copies. Although it has been written specifically for pest control operators, contractors, and others interested in offering protection against house pests, it should be helpful to medical zoologists, public health workers, and students of hygiene. It would be a worthwhile addition to any high school or college library, for even if not studied, much general information can be obtained by even a casual scanning.

More than likely this individualistic book will please some and provoke others. While it contains a great deal of information, its organization may to a certain extent reduce its usefulness. There are five sections to the book, each having its own table of contents and sequence of page numbers. There is no general table of contents at the beginning of the book to direct the reader to the various sections. Furthermore, there are titles to the last four sections and none for the first. The reader must note the items listed in its table of contents in order to ascertain that the first section of 226 pages deals with general information regarding house pests and methods of control. The long index could have been improved if the page numbers had been given more often, instead of references to a more general heading that is often an unfamiliar scientific name of an organism. These features of the book that were found objectionable to the reviewer should not detract too much from its fundamental value. They are nearly all editorial faults that could have been easily corrected by someone experienced in organizing such material.

M. M. Brooke

GENETICS AND CYTOLOGY

Mitosis: *The Movements of Chromosomes in Cell Division. Columbia Biological Series Number XIV.*
By Franz Schrader. Columbia University Press, New York. $2.00. x + 110 pp. 1944.

Mitosis is the ultimate basis of heredity, and the discovery of the forces and mechanisms involved in it is one of the great problems of biology. From the discovery of the chromosomes and the spindle mechanism to the present day, cytologists have not ceased to elaborate hypotheses about the nature of chromosome movements. Yet at the present time, says the author of this monograph, "not one of the many hypotheses that have been broached has in it the definite promise of a final solution. But we have come to realize that mitosis is comprised of a great complex of different mechanisms."

Schrader has produced a survey of present knowledge of the subject of chromosome movements in mitosis that is comprehensive and well balanced, although brief and selective rather than exhaustive in treatment. He has deliberately excluded the reconsideration of work antedating the present half century, and also that summarized in an adequate fashion elsewhere. Although this has saved much space, it has not always worked to advantage. Thus the young student might be misled as to the validity of the electrostatic theories if he failed to consult Wilson's discussion of the subject in *The Cell in Heredity and Development*. The difficulties presented to any such hypotheses by tripolar spindles and the diagonal spindles in quadripolar figures, although still crucial, are not considered in Schrader's monograph. It is only fair to point out that Schrader is careful to make the necessary references, but why Lillie's hypothesis should receive such prominence when the objections to it are left to references is not clear. One wonders whether all the cytologists who have continued to develop new versions of the electrostatic hypothesis have been aware of the fundamental objections to it.

The brief introduction is followed by a chapter on the structural elements involved in mitosis. Evidence from living as well as preserved cells, from unusual and abnormal as well as from normal ones is focussed on the questions of the reality and nature of centrioles, spindle fibers, kinetochores, asters, and spindle constituents. The recognition of two principal types of spindle is in agreement with the views of Bleier, Belar, and others, although the views of Belar on the distinction between the nuclear and cytoplasmic (or "central") components of the spindle are not discussed. The continuous fibers are regarded as cytoplasmic in origin by Schrader, and the chromosomal fibers as nuclear, perhaps, like the interzonal connections, chromosomal. The evidence for the homology of centrioles and kinetochores is also presented.

In the end, none of the hypotheses are satisfactory, although several—contraction and expansion of parts of the spindle, electrical charges, chromosome autonomy, tactoids, etc.—may contain elements of the larger truth. Most of these hypotheses have concerned themselves with metaphase and anaphase movements, and even now we are unable to relate interphase and prophase behavior to what follows later.

In the chapter on related problems, meiotic behavior, telomere attractions, heteropycnosis, and other phenomena are considered. It is here that the monograph seems most curtailed, for while the meiotic mitoses are by no means ignored, the survey can hardly be said to review the extensive subject of chromosome pairing and the role of chiasmata. This is to be regretted, since we would not only like to have Schrader's careful analysis of it and his views about it, but also because of the suspicion that the behavior of the chromosomes in synapsis and crossing over cannot be altogether foreign to their behavior in regular mitosis. If, as Schrader suggests, the most hopeful attack upon the problem may well be that of concentrating on some one phase of the cycle, in favorable material, it might very well be some aspect of the meiotic prophase that would yield the first success.

BENTLEY GLASS

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MEDICAL GENETICS AND EUGENICS.

By Charles B. Davenport, Clyde E. Keeler, Maude Slye, and Madge Thurlow Macklin. Woman's Medical College of Pennsylvania, Philadelphia $1.00. 141 pp. 1940.

This slender volume contains a series of lectures on human heredity delivered at the Woman's Medical College of Pennsylvania in 1940. While geneticists will welcome the signs of growing interest in heredity on the part of American medical schools, these lectures are certainly of very unequal merit, and the lean kine may have eaten up the fat ones. The first three lectures were given by Davenport. In his first, he discusses human variability in physical and mental traits. While recognizing the force of both genetic and environmental factors, Davenport relies chiefly on family pedigrees for demonstrating the role of the former and may be charged with failure to discern the importance of common family influences, education, and social and economic background in molding individual interests and temperament. To say the least, a pedigree lumping incest, epilepsy, feeblemindedness, criminalistic tendencies, and alcoholism has dubious *genetic* significance. Moreover, the pedigrees extend back one or more centuries, cannot be regarded as complete, and certainly depend in most instances on evidence that any critical person would have to reject as unreliable. Just what the pedigrees of notable naval families illustrate, other than the effect of social acceptability on marriage and the effect of family tradition on the choice of a career, it is hard to see.

In the second lecture, there is more of the same—together with an attack on the principle of democratic equality, an attack based on the grounds of the genetic dissimilarity of individuals. But the fortunate diversity of genetic potentialities in human beings emphasized by Davenport was most certainly as evident in the eighteenth century as now, and was indeed at the root of the democratic doctrine of equality of opportunity that has characterized America. If the doctrine of equality has any meaning whatever, it means the equal right of each individual, regardless of color, creed, or nobility of pedigree, to "make the most of himself." Genetic diversity is thus recognized and made the chief pillar of that concern for human individuality and that tolerance of other's differences which characterize true democracy.

Davenport's third contribution is less subject to criticism, its errors being of a more technical nature. His emphasis upon the importance of the genetic constitution in the incidence of disease is certainly well placed. The story he tells of research on mouse leukemia affords an excellent example of what is supposed to be a pathological entity proving upon genetic analysis to comprise a number of diseases. But the statement that hemophilia is "carried in eggs only" is a gross error in describing sex linkage, and the attribution of maternal influence in leukemia "obviously" to the cytoplasm ignores the probable effects of uterine environment or a milk factor.

Keeler contributes a discussion of genes in chemical terms, of gene action in development, and of the meaning of evolution in terms of genes, pointing out the similarity of gene constellations in different mammalian species and the significance of parallel mutation, with the aim of showing why mutants in laboratory mammals are such valuable materials for the study of medical genetics.

Maud Slye, in a concise and excellent account, sums up her work on the incidence of cancer in different genetic strains of mice, presenting evidence for the genetic control of the type of malignancy, of the site of malignancy, and of the age at which malignancy will occur.

The final lecture is by Madge Macklin. In graphic fashion she tells about instances in which an ignorance of genetic knowledge led to medical mistreatment or in which such knowledge pointed the way to correct treatment or advice. She concludes by emphasizing that inherited diseases are not thereby incurable, and that we must have adequate courses of medical genetics in medical schools, as well as centers of research in this most neglected field.

BENTLEY GLASS

MEDICAL GENETICS AND EUGENICS. *Volume 2.*

By R. Ruggles Gates, Laurence H. Snyder, and Earnest A. Hooton. Woman's Medical College of Pennsylvania, Philadelphia. $1.00. 60 pp. 1943.

This second series of lectures on medical genetics to students of the Woman's Medical College of Pennsylvania includes three addresses, given in 1941–1943. In the first lecture (13 pp.), Gates makes a general introductory survey of human evolution, followed by a discussion of the heredity of racial differences and the description of some human hereditary abnormalities of medical interest. Gates is mistaken in saying that a fossil series can be traced from *Australopithecus* through *Plesianthropus* and *Paranthropus* to Rhodesian man, since these South African apes were Pleistocene contemporaries of each other and of man himself.

In the second lecture, Snyder outlines succinctly the practical applications of a knowledge of human heredity in the field of medicine. He discusses instances of autosomal, sex-linked, holandric, and partially sex-linked genes and presents a genetic map of the human sex chromosomes. Linkage, penetrance, expressivity, viability, ontogenetic relations, and gene frequency are other topics considered. One can only wish that this discussion might have been greatly amplified.

The lecture by Hooton emphasizes the universal basis of heredity in physical, mental, and pathological conditions. Hooton overstates his case and underestimates the role of environmental factors. Every "familial" condition appears to him necessarily hereditary, although the story of pellagra makes it sufficiently obvious that families have other common bases, besides genes, for developing common characteristics. Hooton expresses a belief in orthogenesis, yet the gist of his thought seems to be that "some adequate substitute must be found for the obsolete forces of natural selection which in times past have sifted out the inferior human stuff." This he sees in the knowledge and application of human genetics, once geneticists have overcome their "pusillanimity" and doctors their preoccupation with other things. Hooton feels that premedical education should receive a change of emphasis from chemistry and histology to vertebrate comparative anatomy, genetics, physical anthropology, and biometric statistics, and many of us will agree with him on this point. But were he more widely acquainted with genetic work, he would hardly regard the interesting work of W. H. Brown *et al.* on constitutional types and disease proclivities in rabbits as a piece of research *sui generis.* Hooton likes to gibe, to prophesy, to speak *ex cathedra.* One quotation is illustrative and pertinent in present times: "There is but one way to insure peace and that is to extirpate all predacious men and to raise the level of intelligence in human masses to a height where it will no longer be suggestible to the leadership of paranoids and others who lust for power." As a counteractant for this sort of reasoning, one should reread Weinstein's essay *Palamedes.*

BENTLEY GLASS

GENERAL AND SYSTEMATIC BOTANY

THE MYCETOZOA OF NORTH AMERICA. *Based upon the Specimens in the Herbarium of the New York Botanical Garden.*

By Robert Hagelstein. Published by the author, Mineola, N. Y. $6.00. 306 pp. + 16 plates. 1944.

In this compact volume are descriptions of 285 species reported from North America and considered valid by the author, 269 of these having been studied from the representative specimens from North America in the herbarium of the New York Botanical Garden, while at least 216 were also studied by the author in the field and in the laboratory from his own collections and those of his colleagues covering the territory from Quebec to Florida. It is therefore a thoroughly adequate representation of the 318 species that the author considers valid of the total number which have been reported for the world. As would be expected, this authoritative presentation is the result of long continued and thorough investigation. This group for more than twenty years has been the absorbing interest of the author who, in his capacity as honorary Curator of Myxomycetes at the New York Botanical Garden, has had access to the wealth of authentic material from the large original collections of J. B. Ellis and W. C. Sturgis, as well as the thousands of additional specimens received by exchange and donation from correspondents, augmented by the best of the more than 10,000 collections made by the author and by the associates and friends whom his infectious enthusiasm and sincere interest have inspired as collaborators.

After a preface of two pages outlining the background of the work, the introduction discusses the characteristics, nature, method of development, habitats, and occurrence of the Myxomycetes, with methods of collection and study and the bases of classification. There is also a helpful glossary for those to whom the technical terms used in this somewhat specialized group may be unfamiliar. The outline of families and genera follows the accepted classification scheme developed by Lister.

The discussion and description of the genera and species in 258 pages forms the main body of the book. This descriptive treatment is supported by 16 plates, a frontispiece showing the woodland habitats ideal for collecting, while four plates in color from Sturgis' drawings excellently portray the habit of five species especially critical or interesting, as well as the microscopic characters of their spores and capillitium. The remaining plates, 6 through 16, are half-tones of representative fruiting bodies magnified from three to nine times to show their distinctive features. The plates are excellent, the only possible criticism being that there are so few illustrations of the microscopic characteristics of spores, elaters, and capillitia. There are, however, two excellent figures of the characteristic plasmodia. In general the plates are valuable, well chosen, excellently reproduced. The explanations of some of the plates offer more than the usual brief descriptive captions, since they correct errors in the magnification of certain plates by Sturgis when previously published, furnish descriptions for maintaining plasmodia for study, and give the characteristic colors of the specimens photographed.

In the conclusion the author compares the impressive assemblage of forms presented here with those known from other parts of the world and briefly discusses synonymy, distribution, and other general matters of biologic interest.

The extensive and useful five-page list of the literature cited or consulted, prepared by J. H. Barnhart, the Bibliographer Emeritus of the New York Botanical Garden, is appropriately restricted to the taxonomic literature.

The useful index to genera and species lists the accepted names in bold face and the synonyms in italics, while asterisks denote the 33 species not known from North America, as listed on page 274.

The book is an authoritative and complete monographic treatment, a worthy successor to the earlier works of Lister and of MacBride.

In addition to the technical taxonomic descriptive material, there is a wealth of material of general biologic interest. The number of genera with but single species, ranging from *Alwisia* through *Reticularia*, 21 in all, present an interesting contrast to the ten or a dozen genera which have ten to twenty species each, with *Physarum*, as always, far surpassing all others with its total of 62. Speculation as to biologic reasons for the high proportion of monotypic genera in this apparently ancient group would be of interest.

As might be expected, according to the Age and Area Hypothesis, a notable lack of endemism is obvious in this group. There are numerous cases in which the type locality was Java, Ceylon, Tasmania, Paraguay, or similar remote or isolated localities, yet subsequent collections have shown the species to be common in North America and Europe, or even of world wide distribution.

The favorite substrata, dead wood, leaves, and the like, predominate, indicating a notable lack of specialization, since certainly these substrata in Java are not of the same precise composition as the dead wood on which the species appear in the United States. There are also interesting cases of more restricted habitat, the rare *Lachnobolus congestus* having been found twice on old sugar bags. The restriction in substratum shown by *Craterium concinnum*, which, so far as is known, occurs in eastern North America only on decaying chestnut burs of the preceding year and hence has been found only rarely since the chestnut blight almost completely exterminated the sources of such material, and shown by the companion species *Arcyria globosa*, which is found chiefly on chestnut burs but may also occur on weathered leaves of the not too closely related chestnut oak, suggests interesting possibilities of the extinction of similarly restricted species in the past through the extermination of the substratal sources by epidemics.

There is also ample evidence that even in this group, world-wide in distribution and intensively studied, there is still opportunity for the discovery of new and interesting species in woodlots in one's own vicinity.

It is to be hoped that even though one phase of the author's work is completed with the publication of this able book, he will still continue for many years to enrich our literature through further studies of this fascinating and biologically significant group.

Wm. H. Weston

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Mushrooms of the Great Lakes Region. *The Fleshy, Leathery, and Woody Fungi of Illinois, Indiana, Ohio, and the Southern Half of Wisconsin and of Michigan. By Verne Ovid Graham. The Chicago Academy of Sciences and The Chicago Natural History Museum. Chicago.* $4.10 (paper). vii + 390 pp.; 49 plates. 1944.

The author, Honorary Curator of Mycology at the Chicago Academy of Science, conceived the idea of preparing this manual in 1927 when, while giving a course on the fleshy and woody fungi at the University of Chicago, he found it necessary to assemble the publications dealing with those of that region. The present volume, covering the fleshy, leathery, and woody fungi of Illinois, Indiana, Ohio, and the southern half of Wisconsin and Michigan, includes around 1200 species, thus extending not only the scope but also the geographic range of Moffatt's *Higher Fungi of the Chicago Region*, which appeared in 1909 and 1923 and included 400 species.

After a brief three-page preface giving the background of the book and explaining the nature and activities of fungi, there follows a ten-page key to the genera. This key, of the conventional dichotomous type, will probably present unexpected difficulties to the beginner and, since it necessarily employs numerous technical terms, will require support from the dictionary of terms on pages 366 to 370, from plate 1 with its diagrams of various types of fungi, plate 49 with its illustrated glossary of the shapes of pilei, stipes, gills, and other morphological features, and plate 12 with its illustrations of the types of fruiting bodies of the Agaricaceae.

The Ascomycetes are next covered in 29 pages, the five families discussed comprising the more conspicuous forms commonly encountered. The Basidiomycetes, as is natural, occupy the greater part of the book (about 320 pages), and are taken up by families, excluding of course the rusts, smuts, and other forms which do not fall in the category of conspicuous leathery, woody, or fleshy fungi. An index of 17 pages furnishes adequate reference to the genera and species, with helpful inclusion of references to the figures illustrating each. The illustrations, plates 1–49, assembled at the end of the book, comprise collotype reproductions printed at the collotype plant of the museum from figures executed by members of the WPA working from the author's original drawings, from selected photographs, and from specimens in the E. T. Harper collection at the Chicago Natural History Museum. These illustrations, which should be the most effective portion of a book of this type, are in general disappointing. Some are very excellent, others are rather crude and highly diagrammatic and seriously fail to exploit the notable potentialities of collotype as an exquisite medium for the reproduction of scientific material. In general there is a serious lack of the structural details essential to identification. To be sure, in figures 24 and 29 of plate 5 two types of basidia are shown, while in figure 7 there is an attempt to show something of the structural characters of *Hymenochaete*, but these are of little worth in helping the reader visualize numerous essential structural features. The lack of detailed illustrations of the spore characteristics of such genera as *Lamprospora* among the Ascomycetes or *Russula* among the Basidiomycetes, where spore characters are highly significant in diagnosis, greatly curtails the usefulness of the book. To be sure, in plate 40, the illustrations of the fruiting bodies of various species of *Inocybe* are accompanied by drop-like objects presumably meant to be spores, but their vague, uncertain sculpturing and the lack of explanation nullify their usefulness. The plates lack any detailed explanations that might help to supplement their inadequacy and render them more serviceable, the illustrations, in most cases, being merely named without any helpful indication of the distinctive characteristics or structural features significant in identification. The almost complete lack of scales of magnification or reduction is inexcusable; the few that are given increase rather than lessen the confusion.

The book is neither an adequate popular handbook for the use of the interested amateur nor an authoritative regional monograph for the mycologist. For the amateur, although it includes a wider range of fungi, it will by no means prove as useful as the excellent handbooks of Gussow and Odell or of W. S. Thomas. For the mycologist, while it does present under each family a few references to the pertinent monographic literature with occasional references under genera, in general it shows a lamentable lack of the features that are essential to a dependable scientific treatment of any group. One gains the impression that this book cannot be depended upon for sound nomenclature, acceptable treatment of synonymy, or authoritative identification of difficult specimens.

WM. H. WESTON

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THE FLOWERING PLANTS AND FERNS OF MOUNT DIABLO, CALIFORNIA · *Their Distribution and Association into Plant Communities.*

By Mary L. Bowerman. The Gillick Press, Berkeley. $3.75. xi + 290 pp. 1944.

Notable productive activity in the field of botany in California has manifested itself in the excellent monographs, floras, and manuals which have appeared in recent years. To these this book is a useful addition, for it presents an intensive phytogeographical and ecological study of an area distinctive in topography, climate, and soils. The author's work, begun in 1930 and carried on intensively through 1935, led to her doctorate thesis at the University of California in 1936 and with continued work since then has now developed into this book. The stimulating and guiding influence of W. L. Jepson, justly famous for his pioneer investigations and long continued study of the flora of California, is shown throughout.

Mount Diablo, lying thirty miles east northeast of San Francisco, is an isolated peak 3849 feet high, well suited for this intensive study The area covered includes 550 square miles, in which the climate is in a borderline between the cool summer and the hot summer type and the life zone ranges from the Sonoran to the transitional. The illustrations, comprising 26 figures, some line cuts of maps, curves of rainfall, etc., but mostly excellent half-tone reproductions of photographs, vividly portray the diversity of the terrain and the rich opportunities for intensive botanical work.

After considering the physical factors, such as position, topography, climate, soils, and geology with a brief but significant discussion of the paleobotany, the vegetation is studied in detail in Part Two, each of the several formations with its subsidiary associations being adequately discussed, from the broad sclerophyll formation and the deciduous oak conifer formation through the riparian formation of the canyons and gulleys and the formations of the grasslands, the chaparrals, the springs, and the ponds. There follows an interesting and interpretive treatment of the successions which can be traced in the woodland, the grassland, and the chaparrals, with a brief but effective discussion of the effect of fire.

After a brief treatment of the correlation between the vegetation, the soils, and the geology of the region, there follows a highly significant analysis of the content and relationship of the flora. Here the vascular plants of Mount Diablo are shown to comprise 630 species in 83 families, the seed plants comprising most of these with 525 native species, 6 of which are endemics, and 91 that have been introduced mostly from the Mediterranean region of Europe, while the ferns and their allies have a small representation of 14 species and three families. This flora is analysed by altitude, the ranges of its component plants are compared, their origins are discussed, their relation to the character of the terrain, to soil types, and to methods of seed dispersal are noted, and the nature and distribution of the alien elements are examined.

There is a discussion of the collections from the early random gatherings that began with those of the pioneer Brewer in 1861, through the beginnings of more intensive study by Jepson and others from the 1890s, to the more recent work, especially the intensive and comprehensive studies and collections of the author.

The main body of the book presents an annotated catalog of the vascular plants in 176 pages, beginning with an eight-page key to the families or genera, covering the Pteridophytes in four pages, and taking up the families of the Spermatophytes from the Pinaceae to the Compositae in the remaining 172 pages. In this catalog the habitat, associated plants, and specific localities are given for each species, with listings in the order of dominance in the association. Since this treatment is that of a catalog list rather than the descriptive listing of a manual, those not familiar with the species concerned will need Jepson's *Manual of the Flowering Plants of California* or his *Flora of California* to discover the characteristics of the individual species concerned. The plants are quite fittingly considered as components of associations and representatives of localities rather than as botanical entities, although considerable data as to their characteristics may be derived from the keys.

There is a helpful five-page list of literature cited and an adequate four-page glossary of the terms used in the keys, while the index presents both the common and scientific names of the species, genera, and families, thus facilitating ready reference.

All in all, this is a complete, thorough, and vivid picture of the ecology and botany of a distinctive mountain region, and will prove of great value not only to botanists of the vicinity but to those making similar studies of the flora of comparable mountains elsewhere.

WM. H. WESTON

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FLORA OF TEXAS. *Volume 3, Part II. Anacardiaceae, Cyrillaceae, Aquifoliaceae Genus Cuscuta, Convolvulaceae. Volume 3, Part III. Orchidaceae.*

By Cyrus Longworth Lundell and Collaborators. University Press in Dallas, Southern Methodist University, Dallas. Vol. 3, Pt. II, $1.50 (paper); Vol. 3, Pt. III, $3.00 (paper). Pp. 89–150; 151–196 + 34 plates. 1943; 1944.

These two parts follow Part I which, in the first 88 pages of Volume Three, presented Harold N. Moldenke's Eriocaulaceae, Avicenniaceae, Verbenaceae issued in June, 1942. They are a continuation of the flora sponsored jointly by the Southern Methodist University and the University of Michigan Herbarium under the leadership of Lundell, using as collaborators various botanists who are authorities in the taxonomy of the several groups. They follow the laudable plan of presenting descriptions of all the ferns and flowering plants which grow naturally within the state. Of the ten volumes planned, the first and second will give the general discussion of the background of botanical exploration of the state, with keys to families and a complete catalog of the species, while Volumes Three through Ten, devoted to the descriptive flora by families or genera, will be published as parts like these.

Following this plan the Anacardiaceae are ably presented by Barkley of Montana State University, Lundell covers the two species which represent the Cyrillaceae and the ten species of Ilex which represent the Aquifoliaceae, while Yuncker of De Pauw University contributes an effective descriptive treatment, with diagrams of the floral parts essential for the identification, of the 24 species of *Cuscuta* occurring in the state.

Correll's presentation of the 15 genera and numerous species which represent the Orchidaceae in Texas is highly satisfactory. The author's own knowledge of the group, the resources of the Oakes Ames' Herbarium of the Harvard Botanical Museum, and especially the artistically beautiful and scientifically accurate plates, chiefly by Mrs. Ames, with a few by Dillon, combine to form an unusually effective descriptive treatment of the family.

There has in this country been just criticism of the "Fascicle racket" so ably exploited by our European colleagues; libraries and other institutions committed to subscription pay under this instalment system a disproportionately high total price. Similar criticism might perhaps be advanced here, for while many institutions secure this series by exchange, others who pay the set price have already spent $6.00 for the 196 pages that have appeared, leading one to believe that the total for the ten volumes will be high in comparison with such floras as Jepson's for California or Abram's even more comprehensive *Flora of the Pacific States*. The advantages of the system, of course, are the immediate usefulness of the separate parts as issued, without the long wait necessary before such an ambitious and comprehensive work is completed in its entirety.

In any case the appearance of additional parts of this flora will be awaited with interest.

WM. H. WESTON

JOHN MERLE COULTER. *Missionary in Science.*

By Andrew Denny Rodgers III. Princeton University Press, Princeton. $3.75. viii + 321 pp. 1944.

This is an admirable book—a thorough and appreciative biography of one of the great figures in American Botany, a searching and interpretative history of the significant scientific era in which he played an important part.

Here Coulter's life is portrayed from his birth on November 20, 1851, in China, where his father was serving as superintendent of the Mission Press at Ningpo, to his death on December 23, 1928, only five days before the testimonial meeting arranged by the Botanical Society of America to honor him for his many years of leadership and outstanding service in the field of botany. The early influences which shaped him are traced in the first chapter, covering the years at Hanover College in Indiana, from his preliminary training in the Preparatory Department, which he entered at thirteen, to his graduation in 1870 with a thorough background in religion and the classics and an appreciation of the natural sciences; while the next chapter follows his field work as assistant geologist in Utah under Frank H. Bradley in the geologic and geographical survey of the territories in 1872, and his later work in the Hayden Expedition in Colorado, field work which crystallized his intense interest in botany. The account of his early years of teaching at Hanover is illuminating and sympathetic in its portrayal of his youthful limitations and of his energy and courage in starting the Indiana flora and founding in 1875 the Botanical Bulletin, which from 1876, as the Botanical Gazette, kept pace with the development of botany until in 1896, when taken over by the University of Chicago, it had become a leader in its field.

With notable grasp of the subject and understanding of the man, the author traces Coulter's growth to pre-eminence: the Rose professorship of geology and natural history at Wabash College beginning in 1879, with stimulating periods of summer work in 1879 and 1880 at Harvard with Asa Gray, Goodale, Farlowe and others; the presidency of Indiana University in 1891, and of Lake Forest College in 1893, the appointments at the University of Chicago as professorial lecturer in Botany in 1894, and as Professor of Botany in 1896, with the productive years of leadership that ensued until, in 1925, at the age of seventy-four, he retired from teaching to become chief scientific adviser to the Boyce Thompson Institute.

The reasons for Coulter's pre-eminence are well brought out; in him were blended unusual ability as an investigator, an organizer, and a leader; he was a man of vision who grasped and interpreted principles; he was quick to see opportunities for the development of research, was alert to sense developmental trends in the rapidly growing field of botany.

From Coulter as its central figure this historical account extends to such other outstanding contemporaries as Bessey and Farlow, tracing their activities and influences as they interacted with those of Coulter, and showing how the impetus and stimulus of all these pioneers were transmitted and multiplied in the younger men of the rising generations trained and influenced by them.

Even the index of this book is an impressive roster of the botanists and other scientists of the period from 1870 to 1928, an indication of the competency with which this book reflects the personalities, the institutions, the societies, the meetings, the surveys, the publications, the herbaria—all the many aspects of the living and rapidly developing period of science in which Coulter played so prominent a part.

The author is to be congratulated on his success as a biographer, but even more on the grasp, perception, and insight with which, as a scientific historian, he has caught the spirit pervading botany in this active period, the personalities and ideals of the contributing botanists, and the nature of the problems and trends in this era of which they were a part.

The book is a vivid cross-section of the rapid development of botany in America, a development in which Coulter played a leading part. It is eloquent evidence that botany has found in the author a spokesman and historian, and an interpreter of the significance of botanical investigation and of its contribution to the material as well as the scientific progress of a period. It is much to be hoped that the author will continue developing in detail the history of the growth of botany in the United States. With the present volume as convincing evidence of his unusual capability as a biographer and an interpreter, his forthcoming book, *American Botany, 1873 to 1892: Decades of Transition*, will be awaited with eager anticipation not only by botanists but by scientists and historians as well.

WM. H. WESTON

PARASITOLOGY

THE PARASITES OF MAN *in Temperate Climates. Revised.*

By Thomas W. M. Cameron. The University of Toronto Press, Toronto. $3.00. xi + 182 pp. 1942.

As the title indicates, this book is concerned with those parasites of man that are found in temperate climates, primarily those of North America and Great Britain. Exotic parasites are barely mentioned or are omitted entirely. For example, the following are some of those that are not included: *Trypanosoma gambiense* and *rhodesiense*, all of the leishmanias, *Fasciolopsis buskii*, and all of the filarial worms save *Wuchereria bancrofti*. However, quite a number of indigenous organisms that are potential human parasites are discussed: *Apophallus venustus*, *Dicrocoelium dentriticum*, *Metorchis conjunctum*, *Parametorchis complexus*, and *Opisthorchis* *pseudo-felineus.* It is stated in the preface that the book is intended for the practitioner and not for students of tropical medicine, parasitologists, or laboratory workers. In view of the service men returning from the present world conflict, it might be expected that practitioners here at home will be just as likely to encounter one of the known exotic human parasites as one of the potential parasites.

Aside from the above possible criticism, the book definitely fills the need for a textbook that emphasizes the human parasites of temperate climates. Fortunately it is written by a recognized authority on the subject, the Professor of Parasitology at McGill University and Director of the Institute of Parasitology of Macdonald College, Quebec, Canada. One is particularly impressed with the clear concise manner in which the author presents detailed information and fundamental parasitological principles to the reader. For instance, the following is an example of this ability: "The conditions under which helminths cause disease are quite different from those of the protozoa. As with them, however, disease almost always results from numbers, but unlike them, these numbers must all enter from the outside of the host. Thus while a single amoeba may ultimately cause amoebic dysentery, a single hookworm will never cause clinical disease."

Although this book is no doubt written specifically for the author's course in parasitology at McGill University, it might prove suitable for many other similar courses given in temperate climates. The instructor should of course realize the restricted scope of the text and should have more complete reference books available for the student. There are 61 well selected illustrations, a bibliography, and an index.

M. M. Brooke

The Control of Bilharzia in Southern Rhodesia.

By Alan Mozley. Salisbury, Southern Rhodesia. 307 pp. 1944.

A debilitating disease that man is subject to over more than one half of the world is caused by a small worm, *Schistosoma*, and so the disease is called schistomiasis, or bilharzia. In Southern Rhodesia there are two species of *Schistosoma* that infest the blood vessels of man, one found in the intestine and the other in the urinary organs. They enter through the skin, and after some months lay eggs that pass out into water, where they hatch as microscopic embryos that enter snails, each species entering only one of two species of snail. After a few weeks in the snail host, the worms return to the water and perish, within a few days, unless they manage to enter man through his skin.

The author of this book is a malacologist with wide knowledge of water snails in America, Europe, Siberia, and Africa, who went out to Southern Rhodesia with the director of the Ross Institute of Tropical Hygiene, London, to find out what should be done to check this disease that afflicts 35 per cent of the natives and 8 per cent of the Europeans and in some spots up to 90 per cent of the natives. Through 1939 to 1942 thousands of pools and water courses were examined and snails experimented with in a laboratory built for this research. The conclusion was that while the parasite can be killed in man or in the water or in the snails, the best way is to kill the two species of water snail that are necessary secondary hosts for the parasites on their journey from man back to man.

Many experiments made with inorganic and organic substances showed that some would kill the snails without danger to man. Among the plants effective were Eucalyptus, *Tephrosia vogelii* and *Swartzia madagascariensis.* Of this last the pods contain up to 20 per cent saponins (glucosides). But in addition to these substances excellent results were obtained with malachite, which contains copper carbonate and kills the snails when in very weak doses.

Explicit directions for the preparation and scattering of these killing agents are given, along with valuable suggestions for local problems. The natives use some of these plants to kill fish, and posters in their languages urge them to combat the disease with these leaves, and with the malachite they are to obtain from the Government. With native aid the Government may be able to stop the spread of the disease and eliminate it in some localities, and may hope to eradicate the disease eventually.

E. A. Andrews

Parasitic Copepods in the United States National Museum. *Proceedings of the United States National Museum Volume 94, Number 3177.*

By Charles Branch Wilson. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 529–582 + plates 20–34. 1944.

A report completing the identification and description of all parasitic copepods in the United States National Museum. Fourteen new species, six new genera, and the undescribed sex of six other species are described; one new variety, one renamed species, and fourteen other species are also included.

The Argasidae of North America, Central America and Cuba. *The American Midland Naturalist Monograph No. 1.*

By R. A. Cooley and Glen M. Kohls. The University Press, Notre Dame, Indiana. $2.00. 152 pp. 1944.

This first monograph of the American Midland Naturalist is concerned with the soft ticks of the northern and central portions of the Western Hemisphere. It is written by two entomologists of the Rocky Mountain

Laboratory (U.S.P.H.S.) who are authorities on the taxonomy of ticks.

Brief introductory sections are devoted to statements on the medical and veterinary importance of the soft ticks, explanation of morphological terms, and descriptions of techniques for examining ticks. The authors accept four genera in the family Argasidae: *Argas* Latreille 1795, *Ornithodoros* Koch 1844, *Otobius* Banks 1912, and *Antricola* Cooley and Kohls 1942. They present detailed morphological descriptions of the species of these genera that are found in the regions covered by the monograph. The text is illustrated by line drawings and photographs. Spot maps assist in designating the geographical distribution of the species. In all, there are seventy-one drawings, maps and photographs. At the end of the book are lists of the ticks according to their known hosts and distribution in Canada, United States, Mexico, Guatemala, Panama, and Cuba. An extensive bibliography and an index are included.

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MOSQUITO CONTROL: *Practical Methods for Abatement of Disease Vectors and Pests. Second Edition.*

By William Broadbeck Herms and Harold Farnsworth Gray. The Commonwealth Fund, New York. $3.50. xiv + 419 pp. 1944.

All of those engaged in mosquito abatement and malaria control are acquainted with this handbook of Herms and Gray. The enthusiasm with which it has been received is apparent from the four printings of the first edition since it first appeared in 1940. This present second edition, which has been greatly enlarged and brought up to date, will no doubt prove to be even more useful.

The first hundred or more pages deal with fundamental considerations of problems of mosquito control, such as its economic importance, the laws and agencies involved, public education, and preliminary survey work. This portion of the book required very little revision. The subsequent chapters, concerned more directly with the practical application of control methods, has undergone extensive revision and enlargement. This has been necessary largely because of the information that has been obtained during the present war emergency. During the past four years, no doubt more people have been concerned with malaria and its control than during any previous decade. As a consequence a great deal of information has accumulated that is clarifying and expanding our knowledge of the subject. Some of this information has not been released for general consumption, but much of that no longer restricted has been incorporated into this book. For example, the application of D.D.T. as a larvicide is discussed. There are two notable additions to the appendix of the second edition. One is a large folding chart of the important malarial mosquitoes, showing their geographical distributions, typical breeding places, and the effective methods for their control. The second is a section on the identification of mosquitoes. It includes several simplified keys and eleven clear plates illustrating the various morphological structures of the mosquito.

M. M. BROOKE

GENERAL AND SYSTEMATIC ZOOLOGY

SEASHORE LIFE AND PATTERN.

By T. A. Stephenson. The King Penguin Books, Penguin Books, London and New York. 2s. 28 pp. + 16 plates. 1944.

The King Penguins are a growing series of small illustrated books, reminiscent of the prewar German series of the Insel-Bücherei. This particular volume is essentially a collection of decorative illustrations of seashore life. They are accompanied by a brief text in which the artist-biologist discusses how he creates artistic patterns by abstraction from and arrangement of the patterns found in nature. The colored reproductions attain a high standard, and are delightful.

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ENTOMOLOGY FOR INTRODUCTORY COURSES.

By Robert Matheson. Comstock Publishing Company, Inc., Ithaca, N. Y. $5.50. xiv + 600 pp. 1944.

This well illustrated and attractive text is written in a fluent and admirable style. After a general introduction and a consideration of other classes of arthropods the author takes up the external and internal anatomy of insects, devoting an entire chapter to their mouthparts. A chapter on Development and Growth in Insects discusses metamorphosis, chiefly in a descriptive way. The main body of the book is devoted to a survey of 23 principal orders. There is an abundance of keys based on readily apparent structures. The North American species selected as examples have been chosen on the bases of abundance, economic importance, or interesting habits. The book concludes with four chapters on Insects in Relation to Human Welfare, a section that is full of interesting descriptions of insects as food or food producers, as scavengers, and as producers of various useful products; in relation to pollination; and in relation to human or plant diseases. A glossary, bibliography, and index are provided.

The book is a lengthy one, and few students will be able to master more in a single course. Yet, without a desire to cavil, it is disappointing to find here so little on insect physiology, particularly in regard to molting and metamorphosis, so bare a mention of protective coloration and mimicry, of modes of sex determination, or of the genetic and cytological studies that have made insects so important to science. Nor is there very much on the social insects. Perhaps the most startling omission is the failure to consider the basis of behavior and the roles of instinct and intelligence in the varied life histories described.

These are faults of omission only, and with Imms, Wigglesworth, Cott, Wheeler, and others on the reference shelf, too much should not be made of them. The author set out to write an introductory textbook of entomology, and in this he has succeeded well.

Bentley Glass

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New and Little Known Pselaphidae (Coleoptera) from Brazil, Colombia and Mexico, with Keys to Mexican Genera and Species. *Bulletin of the Chicago Academy of Sciences, Volume 7, Number 4.*

By Orlando Park. Published by the Academy, Chicago. Paper. Pp. 227–267. 1944.

Six new species are described, and six are reported from new localities. The pselaphid fauna of the Pacific Slope of Mexico is discussed.

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Checklist of the Coleopterous Insects of Mexico, Central America, the West Indies, and South America. *Part Two. United States National Museum Bulletin 185.*

Compiled by Richard E. Blackwelder. Smithsonian Institution, Washington. 30 cents (paper). Pp. 187–341. 1944.

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Guide to Higher Aquarium Animals. *Bulletin Number 21.*

By Edward T. Boardman. Cranbrook Institute of Science, Bloomfield Hills, Mich. $2.00. 108 pp. 1944.

This attractive handbook on those native vertebrates of Michigan that can be reared in aquaria includes descriptions of one lamprey, twenty-nine fishes, six salamanders, six frogs, two toads, four tree-frogs, five snakes, and six turtles. Most of these forms are illustrated in excellent photographs, and each is briefly characterized as to appearance, size, habitat, breeding habits, and food. There is a short general introduction on aquarium-keeping. Brief appendixes on hardy exotic fishes, on water for the aquarium, and on the treatment of diseased fishes and diseased reptiles and amphibians conclude the book. There is a short bibliography of 22 titles, but no index. However, the table of contents will serve adequately in place of the latter. Teachers and aquarium fanciers should find the volume interesting and useful.

Stingfish and Seafarer.

By H. Muir Evans. Faber and Faber Limited, London. 15s. 180 pp. 1943.

In pursuing the study of fish as a hobby, the British surgeon Muir Evans has concerned himself with diverse problems. This book is devoted especially to the poison spines and other offensive and defensive weapons of marine animals, to the knowledge of which the author has made a considerable contribution. He describes different types of fish, their habits, and the structure and histology of their poison spines and glands, and discusses the nature of the venom and its relationship to pigmentation. The result is a work of practical value, presented as a clear and popular discourse, as free as possible from technical jargon, and with many interesting digressions into related topics that indicate the author's extensive first-hand knowledge of his subject.

Eileen Sutton Gersh

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A Review of the Halfbeaks or Hemiramphidae of the Philippines and Adjacent Waters. *Stanford University Publications University Series. Biological Sciences, Volume IX, Number 2.*

By Albert W. C. T. Herre. Stanford University Press Stanford University, Calif. $1.00 (paper). 48 pp. 1944.

Twenty-four species of this family of fishes are described, along with one doubtful species, one variety, and one new variety. There are no illustrations.

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The Prairie Chicken in Missouri.

By Charles W. Schwartz. Conservation Commission State of Missouri, Jefferson City, Mo. $5.00. 91 pp. + 85 plates. 1944.

This collection of 85 remarkable photographs, including a kodachrome frontispiece, together with five black and white sketches and accompanying text, is an ornithologist's dream. Printed on heavy pebbled paper 9″ x 12″, bound in brown fabrikoid, and published at cost ($3.50), it has been limited to an edition of 2000 copies, a number which will inevitably fall far short of satisfying the demand. The use of the methods of the Limited Editions Club by the Conservation Commission of the State of Missouri in distributing this book of scientific value is to be deplored, especially its limited disposal to individuals at the pre-publication price, and the sale of the remaining 200 to book dealers for resale at collector's prices. It is to be hoped that the Commission will reconsider the matter and make a second printing for wider distribution.

The Wolves of North America. *Part I. Their History, Life Habits, Economic Status, and Control. Part II. Classification of Wolves.*

By Stanley P. Young (Part I) and Edward A. Goldman (Part II). The American Wildlife Institute, Washington. $6.00. xx + 636 pp. 1944.

Wolves belong to the carnivorous family Canidae, which is nearly world-wide in distribution and includes "man's best friend," the dog. Wolves have not only been a menace to human life, but have always been very destructive to domestic stock, being perhaps the most efficient of all predators. In ancient legends the wolf already figures as a symbol of sagacity, courage, and ruthlessness. Only in recent days and with the aid of modern traps and poisons has man succeeded in exterminating the wolves over a large part of their historic territories. From the point of view of human welfare, economics, history, and literature the wolves and their descendants, the dogs, represent the most important and interesting group of carnivores.

This large and scholarly volume deals with the two North American species of wolves, *Canis lupus* and *Canis niger*, but not with the closely allied coyotes. In the first two thirds of the book Young reviews the historical references to American wolves and discusses their past and present distribution, habits, economic status, and control. The second and smaller part, written by Goldman, is devoted to the taxonomy of the wolves in the New World.

Not long ago wolves still ranged over nearly all the vast land from the arctic zones to central Mexico, but to-day they have disappeared east of the Mississippi, excepting in northern Wisconsin and Michigan, and from most of eastern Canada and all of Newfoundland. Wolves begin to breed in their third year. The period of gestation lasts 60 to 63 days, and an average of seven whelps are born some time between April and June. A fully grown wolf, weighing about a hundred pounds, can gorge itself easily with eighteen pounds of meat at one meal. Wolves have very powerful jaws and effective dentition. One trapped animal severed with one snap a knotty juniper limb, two inches thick. In old wolves, i.e., after the age of about 12 years, the teeth become much worn and lose their cutting power, but the animal can still grab his prey by the throat and succeed in strangling it. The diet of wolves forms a long and varied list, ranging from berries, fishes, frogs, and birds to elk, moose, horse, and steer. It includes carrion, and even the wolf itself. Monetary losses to ranchers caused by wolves, after the buffalo had been replaced by cattle and sheep, reached huge sums. It led to the relentless pursuit of the killers by means of all sorts of devices, backed by high bounties, devices ranging from baited fishhooks, suspended from trees, to deadfalls, pits, wolf-scented traps, drives, and, most deadly of all, poisons. Wolf pelts repay only a small part of the cost of wolf control. Between 1738 and 1747 the Hudson's Bay Company alone sold over 10,000 wolf skins at prices varying between 9 and 18 shillings apiece, but in 1938, when few skins reached the markets, the price had risen to as high as 65 dollars for a prime pelt. That wolf and dog will cross readily and produce fertile offspring has been amply demonstrated.

In *Canis lupus* 23 subspecies can be distinguished; in *Canis niger*, 3. The two species and their numerous geographic variations differ quantitatively, rather than qualitatively, in regard to general size, color, detailed shape of the skull, and diameters of the molariform teeth. Individual variations in all these features are common and marked; in regard to coat color they can range from nearly white to almost pure black. It appears that the different local races intergrade extensively. This is shown for cranial characters by the long tabulations of measurements accompanying the taxonomic report.

The facts mentioned above are mere random samples of the great mass of detailed and comprehensive information, collected in this useful monograph on North American wolves. The book is generously illustrated by text figures and 131 plates. Of special value is the bibliography, filling 80 pages. Unfortunately there are no summaries, and the index is far too brief for such a large reference work.

Adolph H. Schultz

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Laboratory Manual for Introductory Zoology.

By C. Courson Zeliff. Published by the author, Harrisburg, Pa. $1.50 (paper). 144 pp. 1944.

This manual is for a full year course. It includes studies of cells, tissues, mitosis, gametogenesis, and embryology, and a very extensive survey of the animal phyla. Directions are clear, concepts modern. There is no physiology, no genetics, no field work. A few illustrations are included.

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ANIMAL EMBRYOLOGY

Experimental Studies on Ectohormonal Control of the Development of Supplementary Reproductives in the Termite Genus Zootermopsis (Formerly Termopsis). *University of California Publications in Zoology, Volume 43, Number 17.*

By S. F. Light. University of California Press, Berkeley and Los Angeles. 50 cents (paper). Pp. 413–454. 1944.

Numerous experiments failed to supply conclusive evidence in support of the ectohormonal theory of reproductive inhibition, but the general trend of the evidence is favorable to it.

ANIMAL MORPHOLOGY

Speed in Animals: ***Their Specialization for Running and Leaping.***

By A. Brazier Howell. University of Chicago Press, Chicago. $4.00. xii + 270 pp. 1944.

This book will be an anatomist's delight, for it is mostly anatomy, nearly naked and quite unashamed. The title however, is apt to be misleading. It should be "The Anatomical Basis of Speed in Vertebrates"—in fact, "in Mammals," for the reader will look here in vain for any information about the running and leaping of those groups of insects that are specialized for exactly that mode of locomotion, to say nothing of the controversial speeds of the deer botfly or the squid. Fish are treated briefly, omitting almost entirely the kind of work represented by J. Gray. Birds receive a disappointing two and one-half out of 262 pages. But to complain of this is to ask for another book. Once it is realized that this volume is frankly an account of those aspects of the subject that have been "of greatest interest to [the author] individually," the reader will gladly discover a great mass of anatomical facts about the bones and muscles concerned with locomotion, and something about various types of locomotion found in mammals.

After a description of the adaptations for speed and locomotion generally in the monotremes and the marsupials, the more important orders of placental mammals are discussed. This is followed by special chapters on the muscular system, the axial skeleton, the fore limb, the hind limb, proportions, and gaits. There is considerable emphasis, legitimately, we believe, on the horse. Altogether, an enormous number of facts have been gathered together around the concept of adaptation for getting from one place to another.

The author leaves for others a consideration of the physiological, neurological, endocrinological, and other aspects of speed in mammals. It is to be regretted that he did not treat the evolutionary explanation of these adaptations in the same way. The text is marred by recurring references to "the need for speed" and the varying ability of different evolutionary strains to "respond to it," or the "evolutional effort" that has gone into the anatomical specializations now existing. Such remarks, and others like them, are possibly intended as metaphors, a mere manner of speaking. Nevertheless, they will most certainly make anyone wince who knows something about the facts of genetics or the modern theories of evolution. A layman would surely be misled.

We were sometimes puzzled about the public for which the book is intended. On some pages even the most elementary words are most fully explained; on others a flood of technical terms is introduced with little or no prior explanation. What must happen to the reader who needs to be told the meaning of the origin and insertion of a muscle (both of which are fully explained) when he suddenly reads that the fibula is not supported by the calcaneus, that the astragalus has but a single pulley and rests solely on the navicular, and that the mesaxonial is such that the axis of the podial passes through the third digit? There should have been at least a glossary. Many topical comments suggest themselves. The account of camels and camel racing is noteworthy. The various gaits of horses are especially clearly described and illustrated with drawings made from frames of a slow motion picture. Perhaps, on the whole, the book has the faults of its virtues.

The illustrations are both pleasing and clear, though not very numerous, especially in view of the price of the book, which seems excessive.

G. B. Moment

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Topographical Anatomy of the Dog. ***Fourth Edition.***

By O. Charnock Bradley. Revised by Tom Grahame. The Macmillan Company, New York. $7.50. xii + 316 pp. 1943.

Since the dog is one of the most widely used experimental animals, a first-class account of its anatomy is especially to be appreciated. That Charnock Bradley's well-known handbook, the English equivalent of Ellenberger and Baum's *Anatomie des Hundes*, now appears in its fourth edition is in itself ample testimony of its proven worth. In some respects it is a more useful work than its German counterpart.

The present edition represents a considerable revision, including a rewriting of certain parts and the introduction of some excellent x-ray photographs and new diagrams. The illustrations are uniformly of high caliber. The presentation remains topographical rather than systematic. Some subdivision of the text on the basis of regions, however, would have enhanced the utility of the book. There is one notable instance of regrettable terminology—perpetuation of that curious error of nomenclature, "nervi cerebrales" (in place of "nervi craniales"), perpetrated by the B.N.A.

W. L. Straus, Jr.

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Bailey's Text-Book of Histology. ***Eleventh Edition.***

Revised by P. E. Smith and W. M. Copenhaver, with the assistance of Aura E. Severinghaus and Charles M. Goss. Williams & Wilkins Company, Baltimore. $6.00. xx + 786 pp. 1944.

That this book, which first appeared just forty years ago, has gone through eleven editions, is a sufficient indication of its value. It has long been one of the most popular histological texts, especially in medical schools. No doubt its popularity deservedly will be continued.

The new edition has undergone considerable revision. Many new figures, both in color and half-tone, have been included. The text has been brought up to date and extended by incorporation of recent work. A section on the placenta has been added. Selected references to the literature are appended to each chapter.

ANIMAL PHYSIOLOGY

The Living Body. *A Text in Human Physiology. Revised Edition.*

By Charles Herbert Best and Norman Burke Taylor. Henry Holt and Company, New York. $3.90. xxii + 571 pp. 1944.

In its revised edition, this book remains firmly among the leaders of its kind, and perhaps is without a peer. A shorter text of physiology, it is written primarily for use in college courses in human physiology, but also for courses given to nurses and dental and agricultural students. As such, it is necessarily condensed and dogmatic in contrast with the longer physiological texts. It is not, however, merely a condensed version of the larger, excellent treatise by the same authors, but has its own flavor. The simple, lucid, yet scholarly manner of presentation make it ideally adapted to its purpose.

Although the accounts of the functions of the various tissues and organs are preceded by descriptions of their structure, many of these are frequently all too brief or inadequate. At least this is true, in the experience of the reviewer, in respect to its use in courses in combined anatomy and physiology given to student nurses, who have need of something more than the most sketchy account of human anatomy. Because of this, it is difficult to use the book as a basic text, although it is excellent for collateral reading. This would apply to both the original and revised editions, for the latter has undergone no fundamental change in this particular feature.

The revised edition does contain, however, much new physiological material based on work that has been done since the book was first published in 1938, material relating to such subjects as hemoglobin, transfusions, clotting, hypertension, respiration, and vitamins. The 283 illustrations are uniformly well chosen and executed with great clarity.

W. L. Straus, Jr.

Medical Aspects of Aviation (Speed and Acceleration).

By Capt. Ernst Jokl. Sir Isaac Pitman and Sons, Ltd., London. 10s 6d. xiii + 104 pp. 1943.

The title is an overstatement of the scope of this little book. The author proposes to describe the medical problems of modern aviation, chiefly those created by speed and acceleration, to pilots, Air Force officials, medical practitioners and educated laymen. His simple, direct statements of the physical and physiological stresses encountered in modern aviation are for the most part clear and accurate. Numerous illustrations and accounts of experiences attract the reader's attention, and no one could fail to understand this discussion. One hopes, however, that the medical profession and Air Force personnel have advanced far beyond the need for such an elementary presentation of the physiological problems created by such factors as speed, acceleration, and exposure to high altitude. An educated layman will find little in this volume which he does not already know. Those who are actually dealing with aviation and aviation medicine can find other reviews and books that will be of much greater interest and aid.

Physiology in Aviation.

By Chalmers L. Gemmill. Charles C. Thomas, Publisher, Springfield, Illinois, and Baltimore. $2.00. vii + 129 pp. 1943.

This is a well-conceived small handbook designed to familiarize aviators with the changes in body function that tend to occur under conditions encountered in aviation. Such topics as the control of respiration, the carriage of oxygen by the blood, the effects of anoxia, aeroembolism, the effects of acceleration on man, temperature control, the physiology of muscular exercise, and others are clearly and briefly dealt with. Although the treatment of important problems is sketchy, this book would be very useful to physicians and excellent for the preliminary training of students, were it not for one defect. The carelessness of preparation has been such that both minor and major errors of grammar and fact occur throughout the book in such numbers that they cannot be ignored. The author has appended a list of thirty-seven corrections, but this list does not correct all the errors. No acknowledgments of the sources of the charts and tables used are given. Most of the graphs and many of the tables contain no statements as to units used, and even one who is familiar with the subject has difficulty in understanding them. If this book were corrected and reprinted, it would be useful to those interested in physiology and aviation.

Secretory Mechanism of the Digestive Glands.

By B. P. Babkin. Paul C. Hoeber, Inc., New York and London. $12.75. xix + 900 pp. 1944.

The author has not attempted to review the whole of the literature concerned with the secretory function of all digestive glands. The material presented here has been derived chiefly from the work performed during recent years by the author and his associates. The book deals mainly with the mechanisms regulating the secretory functions of the gastric, salivary, and pancreatic glands, while other digestive glands are dealt with to a lesser extent. The first five chapters are devoted to a discussion of the morphology of the secretory glands of this system. The next fifteen chapters describe the innervation, blood supply, secretory activities, and general function of the stomach. This group of chapters concerned with the gastric phases of the digestive process is followed by four chapters enumerating the hormones of the alimentary canal and their contribution to pancreatic, intestinal, and gastric function. The remaining chapters are devoted to a description of the regulation of salivary secretion, except the final two, which return to a discussion of the secretory process and the effects of nerves on the digestive glands. The reader is aided from time to time throughout the book by summaries of the conclusions that may justifiably be drawn from the data presented. In dealing with questions concerning which the available information does not permit a decision concerning the nature of the basic mechanism, the author presents the current hypotheses and the evidence pertaining to their validity. The analysis of the neural and chemical control of gastric secretion is detailed and clear, and, like the author's treatment of all the selected subjects, admirable. One of the most impressive features of this work is its completeness and comprehensiveness. No aspect of function, from the processes within individual cells to the functions of the organs and the intricacies of the controlling mechanisms, has escaped his attention. The bibliography is extensive and the index adequate. However, in seeking information concerning specific points, one must search the entire volume because various aspects of function are treated in several connections. Some individuals may not agree fully with certain of the author's interpretations, but it is inconceivable that any should feel other than admiration for this excellent treatise.

CHANDLER McC. BROOKS

HEALTH AND DISEASE

MEDICAL EDUCATION IN THE UNITED STATES BEFORE THE CIVIL WAR.

By William Frederick Norwood, with a foreword by Henry E. Sigerist. University of Pennsylvania Press, Philadelphia; Oxford University Press, London. $6.00. xvi + 487 pp. 1944.

As this history ends long before the great reforms in the field of medical education, it contains, besides a description of brilliant beginnings in the 18th century, mainly the history of the "dark ages" of medical education in the United States. It is thus less a contribution to the history of medical progress, than to the history of civilization in this country. The author has collected with great industry the already existing but so far widely dispersed material on the numerous old American medical schools, many of them now extinct and to this he has added the fruits of his own extensive research. He has thus created a very valuable and reliable survey of a subject, which probably because of its being controversial up to a few decades ago, has attracted the attention of those interested in medical history almost more than the history of medicine proper, that is, the history of diseases and their treatment.

ERWIN H. ACKERKNECHT

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X-RAY EXAMINATION OF THE STOMACH. *A Description of the Roentgenologic Anatomy, Physiology, and Pathology of the Esophagus, Stomach, and Duodenum.*

By Frederic E. Templeton The University of Chicago Press, Chicago. $10.00. iv + 516 pp. 1944.

The aim of this book, as stated by the author, is to describe and deal in considerable detail with the newer x-ray techniques employed in examining the esophagus, stomach, and duodenal bulb, together with the clinical interpretation of the findings. This has been accomplished in a satisfactory manner. Descriptions of apparatus and examination procedures are given in the first four chapters. The fifth chapter describes in detail the normal anatomy and activities of the pharynx, esophagus, stomach, and duodenum. The remaining thirteen chapters are devoted to a very thorough discussion of the identification of the abnormalities produced by operations, neuromuscular disturbances, inflammations, peptic ulcers, neoplasms, and other pathological and nonpathological processes. Descriptions are extremely thorough and the illustrations are numerous and excellent. This book is highly recommended to those engaged in x-ray examination of the stomach. Anatomists, physiologists, and others who deal with the function of the gastro-intestinal system can also obtain much information from it, but these contributions are scattered and limited. For example, the physiologist will find that the motor activities of the esophagus and stomach which can be visualized by means of the x-ray technique are very thoroughly described and portrayed, but the discussions of their origin, control, and the causes of abnormalities are brief and not easily found. This book is a worthy contribution to the advance of roentgenology and should be a great aid to gastro-intestinal diagnosis.

CHANDLER McC. BROOKS

* * *

HYPERTENSION AND HYPERTENSIVE DISEASE.

By William Goldring and Herbert Chasis. The Commonwealth Fund, New York. $3.50. xv + 253 pp. 1944.

This book is the product of fifteen years of collaboration between the Departments of Medicine and Physiology of the College of Medicine of New York University. By design the work is a description of the authors' concepts of hypertensive disease, and the bulk of material presented is derived from their own clinical and experimental observations. As such, it is a clear and confident analysis of evidence concerning the cause, nature, and treatment of hypertensive disease. It is initially stated that the fundamental hemodynamic alternation in hypertension is an increased resistance to the outflow of blood in some greater or lesser portion of the systemic arterial bed. The essential criterion of the diagnosis of hypertension is abnormal elevation of the diastolic blood pressure. In hypertensive disease, due to the operation of those factors that normally control arterial pressure, it is illogical to conclude that variations in blood pressure are due to changes in primary disturbance or to use the level of blood pressure as an indication of the progress of the underlying disease. Rational therapy must be directed towards the still unknown mechanism which precedes vasoconstriction and the consequent elevation of pressure. The authors next discuss the clinical aspects of hypertensive disease and give a description of kidney, heart, retinal, and brain involvements. The concept of a prehypertensive phase is discarded as unsubstantiated. The following chapters, which are devoted to a description of the results obtained from well-performed measurements of cardiac output, arterial blood pressure, effective peripheral resistance, renal functional and hemodynamic alterations in hypertension, are admirably clear and convincing. The techniques used are described in the appendix. The chief theme of the book is stated in chapter six, in which the work on experimentally produced hypertension is briefly reviewed and compared with clinical observations Here it is admitted that a primary renal mechanism has been established in the genesis of experimental renal hypertension, and that hypertension might be produced in man by the same technique. However, clinical evidence as analysed does not support the concept that renal ischemia is the primary etiological event in human hypertensive disease. The renal ischemia observed in hypertensive patients appears to be one of the sequelae of the hypertensive process. The authors' evaluation of medical and surgical treatment will disappoint many who have claimed high degrees of success from various procedures. The use of thiocyanate in hypertensive patients is held to be unjustifiable. Pyrogenic substances produce temporary lowerings of blood pressure, accompanied by various degrees of amelioration of symptoms, without, however, producing a correction of the fundamental disturbance. Treatment with renal extracts is held to be of benefit probably only because of pyrogenic reactions. Treatment with amine-oxidases have failed. Sympathectomies are in no sense a cure of hypertensive disease. Unilateral nephrectomy, omentopexy, nephropexy, and other surgical procedures are of no demonstrated value. These generalizations are abruptly reached, but the reasons upon which they are based are stated.

The conclusion one draws from this treatise is that the primary cause of hypertensive disease in man is still unknown. All the medical and surgical treatments thus far introduced are of no value in correcting the primary dysfunction, although they may evoke transient ameliorating effects by producing compensatory changes. The device proposed as the most valuable in rehabilitation of the hypertensive patient is psychotherapy. Though the general tone of the book may be displeasing to those whose hypotheses have been so briefly dismissed, it will be generally agreed that a concept of hypertensive disease has been well presented and skilfully supported, both by experimental evidence and by clinical observation.

CHANDLER McC. BROOKE

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YOUR EYES.

By Sidney A. Fox. Alfred A. Knopf, New York. $2.75. xiii + 191 + viii pp. 1944.

This is a fluently written and readable book for the layman, presenting in readily comprehensible form the answers which in the present state of knowledge can be given to the common questions that laymen ask about eyes and vision. The mechanism of vision, of light and dark adaptation, and of color vision is discussed. A simple outline of refraction is given, together with a discussion of why some people need glasses. The problems of illumination, of glare and sunglasses, and of the visual requirements of automobile driving are discussed. Simple and reasonable suggestions are included concerning the hygiene of the eyes and first aid for injuries. The most frequent diseases that require surgical treatment are discussed, and the layman is given an outline of what can reasonably be hoped for under competent care.

In addition, there is an excellent chapter on the most flourishing current quackeries regarding the treatment of eye defects. There is also a valuable chapter clarifying the distinction between optometrists and eye physicians. It is well that the layman should know that optometrists are not only untrained in the recognition of diseases of the eye, but are actually legally exempted from any responsibility in case a patient loses his sight as the result of their having incorrectly told him that his eyes were healthy. It would also be well for the layman to know that there are some physicians who practise as eye specialists without any special training in this field. State Medical Boards give identical examinations and identical licenses to those who become general practitioners and to those who become specialists, and there is no legal restraint preventing any licensed physician from calling himself a specialist. As the author wisely points out, the layman should ask his family physician for advice in selecting a specialist.

It is to be regretted that a chapter is not included on the cost of eyeglasses, a story involving price fixing and rebates in which neither optical manufacturers, optometrists, nor eye physicians are free from responsibility.

JONAS S. FRIEDENWALD

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FERTILITY IN MEN. *A Clinical Study of the Causes, Diagnosis, and Treatment of Impaired Fertility in Men.*
By Robert Sherman Hotchkiss, with a Foreword by Nicholson J. Eastman. J. B. Lippincott Company, Philadelphia. $3.50. xiii + 216 pp. 1944.

The National Committee on Maternal Health, as part of its program of promoting studies on human reproduction, has sponsored the publication of two volumes, of which this book is one, on the problems of sterility. Its author is a genito-urinary surgeon who has for twelve years conducted a pioneer clinic for male sterility. With the aid of the National Committee on Maternal Health he has had excellent research associates. He is evidently an enthusiastic student, an ingenious surgeon, and a humane practitioner. That part of the book which deals with clinical diagnosis and treatment represents careful thinking and thorough study of the individual patients. The delicate social and psychological problems which present themselves in this field of practice are sensibly and sympathetically treated. There is a full and interesting discussion of John McLeod's researches on the metabolism of spermatozoa, of the author's own studies of the variability of human semen, and of other recent work closely relevant to the practical problem.

Readers should be warned, however, that this book is not the place in which to study the general background of the problem of male infertility. As soon as the author gets away from his own immediate experience he becomes inaccurate and obscure. Part of this is due to poor writing. Merely inept English, which occurs on almost every page, may be forgiven to an author distracted by active military service, if not to the publisher and sponsors; but the language frequently confuses or obfuscates the reader, as on p. 33, where it is implied without reservation that sterile couples who adopt infants have children of their own shortly thereafter; or on p. 16, where it is said that "laboratories have found regular descendants of sterile males in colonies of mice." The account on p. 195 of the Rh factor, important as a possible cause of human sterility, is not intelligible. In other places it is clear that the author has tried to round out his discussion by introducing topics from basic sciences which he has not had time to assimilate, witness the passage on "heredity" (i.e. sterility due to genetic causes) which contains two gross misstatements, or the paragraph on the history of the male hormones, which fails to make clear the nature of Berthold's fundamental contribution and omits all mention of the fundamental chemical work of McGee and Koch.

In summary, this book contains valuable information for practitioners dealing with male infertility; properly pruned and edited it would be an excellent clinical textbook; but if the Committee on Maternal Health wishes, as it presumably does, to stimulate the interest of the medical profession in fundamental scientific problems in this field, so that clinical study may go forward on a sound basis, its purpose would have been better served, and the valuable experience of the author more fairly represented, had his contribution been given its proper place as part of a volume prepared by a group of specialists in the several aspects of the subject.

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FERTILITY IN WOMEN. *Causes, Diagnosis and Treatment of Impaired Fertility.*
By Samuel L. Siegler. Foreword by Robert Latou Dickinson. J. B. Lippincott Company, Philadelphia. $4.50. xv + 450 pp. 1944.

This is the companion volume to *Fertility in Men*, reviewed above, and like that volume represents the practical experience and the thought of an active specialist in the disorders of human reproduction. Practitioners in this difficult field will find in it a great deal of information on diagnosis and treatment. The program of study of the individual case is fully analysed. Technical procedures are carefully described. There is a good chapter on tubal insufflation ("Rubin test") and on hysterosalpingography (visualization of uterus and tubes by x-ray), the latter subject being illustrated with interesting roentgenographs. Treatment with ovarian and pituitary-type hormones is conservatively discussed.

Dr. Siegler quite properly views sterility in women as a biological problem and seriously tries to found his exposition upon the existing body of physiological knowledge. In this effort he has, however, wandered far from his own personal field of experience, to treat of biological and chemical matters at second- (and sometimes at third-) hand. The compilation resulting is not clearly focussed on the immediate problem, nor is it free from confusing minor errors and half-truths. The book cannot, therefore, be recommended without reservation to students of biology and medicine as a source of information on the general biology of human sterility.

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THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. *A Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, Etc., with the Pronunciation, Derivation, and Definition. Twentieth Edition, Revised and Enlarged.*
By W. A. Newman Dorland, with the collaboration of E. C. L. Miller. W. B. Saunders Company, Phila-

delphia and London. Plain, $7.00; thumb-indexed, $7.50. 1668 pp. 1944.

In this new edition the editors have followed their policy of presenting a revision of this standard reference work every three years. By eliminating some of the tables and portraits, they have made room for many new definitions without perceptibly enlarging the volume. New terms from biochemistry, chemotherapy, tropical and parasitic diseases, vitamin research, endocrinology, mycology, and especially from war medicine and surgery have been added.

General biological terms are defined so wholly from a medical standpoint that as general definitions many are unsatisfactory; a number represent antiquated conceptions—mitotic prophase, for example. It is also surprising that virtually no account has been taken of the developing knowledge of the hereditary aspects of many of the diseases listed. A few are said to be "hereditary" or "familial," but without any more specific definition of their mode of inheritance. So little effort has been made to modernize the dictionary in this respect that the criticism is true not only in instances where the mode of inheritance is doubtful, but even for such well established cases as the ordinary blood groups, the Rh factor, retinitis pigmentosa, and red-green colorblindness.

In spite of these shortcomings, this dictionary will be almost as useful on the desk of the biologist as on that of the medical student or practitioner.

BENTLEY GLASS

ANIMAL NUTRITION

AN INTRODUCTION TO FOODS AND NUTRITION.
By Henry C. Sherman and Caroline Sherman Lanford. The Macmillan Company, New York. $2.50. viii + 292 pp. 1943.

This book is a timely one. It has been written, as the authors say in their preface, "to aid the solution of the practical problems of adjustments to the food supply and rationing conditions of today and tomorrow and to develop the educational value of resourceful use of nutritional knowledge in a changeable situation as to availability of individual articles of food."

To achieve the purpose stated above, the authors have divided their book into four main parts, namely:

I. Individual and National Importance of Nutrition.
II. The Maintenance of Good Family Nutrition; Difference in Need due to Age, Sex, and Occupation.
III. Foods: Their Properties, Preservation and Preparation.
IV. Planning of Meals and Management of Food Supplies.

In the first part there has been included a brief discussion of the standards of good nutrition, the food needs of the individual, and the proper food selection to maintain good nutrition. A discussion of the national nutrition problem, including quotations from the first National Nutrition Conference, held in Washington, D. C. in May, 1941, is included.

The second part of the book includes a very brief discussion of the essentials of an adequate diet: calorie value, proteins, vitamins, and a few of the minerals. This part of the book contains the essential information written in a simple way for a non-scientific person. Detail of any kind is lacking.

The third division of the book contains much excellent information about foods. There are chapters devoted to "Milk and Its Products," "Meats, Fish, Poultry, Eggs and Nuts," "Fruits and Vegetables," "Breadstuffs and Cereals," "Fats and Sweets," "Food Adjuncts," and "Preparation of Food to Retain Nutritive Values." These pages are filled with instructive data about these foods, both as to the production of them, and their nutritional value.

The last division of the book includes a discussion of meal planning and gives a few sample menus.

The last chapters of the book deal with budgeting and purchase of foods. The authors limit themselves to a discussion of this chiefly "from the viewpoint of so investing the money available for food as to secure the best results in nutritional well-being." Some information is included about the grading and standardization of fruits and vegetables.

The book is concluded with a discussion of the individual and public nutrition policy: "Undoubtedly any sound nutrition policy, whether individual or national, and whether for the immediate situation or for a permanent future, should take due account of the findings of recent scientific research."

This book is written in an interesting, clear style, is concise, and contains much useful information. At the end of each chapter, there are exercises for the reader to use to test his understanding of the information given in the chapter. There are also listed "Suggested Readings," with very helpful comments by the authors on the listed articles.

In their preface the authors state that "This volume seeks to serve anyone interested in foods and nutrition, whether or not with a background of previous study of science." Because this purpose is so well achieved, the book would not be an adequate text for a scientific nutrition class, but it could easily be used in nonscientific groups.

MARGUERITE M. SCHMIDT

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NEW ASPECTS OF CHEAP FOOD: *with a Table of Foods in alphabetic order showing in a single figure the comparative value in nutritive units of potato.*
By Rudolph Keller. Research Books, Ltd., in association with Wm. Heinemann, London. 1s 6d (paper). 52 pp. 1943.

This pamphlet is a paper-bound war edition of 50 pages, written by a professor from the University of Prague now living in England. There is apparently no plan of organization in this pamphlet. It consists of a group of twelve articles, in which the author airs his views and grievances. Apparently he is attempting to improve the English dietary in their rationed country, for he gives some general rules which the British should follow. These are good enough rules, but are not as complete and adequate as those which we in America advocate.

The author also attempts to give in one figure an estimate of the nutritional value of food. "This estimate is based on a comparison with potatoes, today the staple food of the poorer part of the community and thought to be the cheapest food, which it is not actually."

The pamphlet is poorly written, and the information not well expressed. In fact, it is so poorly expressed that on first casual reading one thinks that many of the statements are in error, until one perceives their real meaning. There is little of value in this pamphlet, particularly for those outside of England.

Marguerite M. Schmidt

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GENERAL PHYSIOLOGY

Medical Physics.

Edited by Otto Glasser. The Year Book Publishers Inc., $18.00. xlvi + 1744 pp. 1944.

This book is an ambitious attempt to supply, in the form of an encyclopedia, a text and a working manual for the application of physics to medicine. An extensive amount of information has been collected by Dr. Otto Glasser, Editor-in-Chief, and his twenty-three co-editors on many physical and physical-chemical phenomena of importance in medicine; much of this information would be difficult to locate unless very extensive library facilities were available. The field of application of physics to medicine is so wide that it is hardly possible to cover it in one volume. It is for this reason rather surprising that 53 pages are devoted to "bioelectricity," many phases of which are also discussed under different headings. In contrast to this, only 6.5 pages are spent on colloid chemistry and nine pages are given to "cosmic rays," a subject which at present is of very limited interest to medicine. The use of radioactive tracers in biological work—a subject of great immediate importance to medical research—is discussed in two pages.

The usefulness of this volume as an encyclopedia is reduced considerably by the peculiar arrangement of literature citations, which are 1) arranged in alphabetical order by the names of the senior authors; 2) each preceded by a number following the consecutive order of the first use of the references in the text. Since the name of the author of the reference is often not used in the text, but the number only, it makes it difficult to locate a reference in the bibliography.

Some chapters carry practically no references; for instance, the chapter on disinfection (one reference) and the chapter on the electron microscope. This latter chapter discusses the product of one manufacturer only. Very little reference is made to previous models, some of which have proved quite successful in electron microscopy.

The omission of many topics which could be useful in such a volume can probably be explained by the fact that investigators, who in 1940 were quite ready to contribute a chapter to this volume, found themselves in 1943 involved in war work that made it difficult to fulfil their promise.

The editor and publishers are to be congratulated for their courage in bringing out such an extensive volume under war conditions. It is very much to be hoped that a more balanced distribution of topics can be accomplished in successive editions.

The volume, with its wealth of information, has already proven to be of great help in the reviewer's laboratory. It can be highly recommended to anyone who is interested in the application of physics to medicine.

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BIOCHEMISTRY

Annual Review of Biochemistry. *Volume XIII. Edited by James Murray Luck and James H. C Smith. Annual Reviews, Inc., Stanford University P. O., California.* $5.00. ix + 795 pp. 1944.

This volume contains much that will be of interest to biologists. It is evident from these contributions that the productivity in this field has not been diminished. In reviewing such a group effort, it is impossible to make general statements that will apply to all chapters. It is, however, possible to place review articles in one of two groups. The first group contains reviews that may be called annotated bibliographies. The second group contains reviews in which a large amount of factual material has been arranged and presented in a clear, critical, and discerning manner that is possible only when the author has a profound knowledge of the field. This year's review contains many contributions in the latter class. Some of those that are of greatest interest to biologists will be mentioned in this review.

"Biological Oxidations and Reductions," by D. E. Green and P. K. Stumpf, brings up-to-date Green's excellent book on this subject. The discussion of "Non-Oxidative Enzymes" by Mann and Lutwak-Mann is a discussion of enzymes of another type and includes much material on phosphatases and choline esterase. The review of the work bearing on the structure of the intact protein molecule, by Neurath and Greenstein, belongs to the group of discerning reviews.

The review by Koch of recent chemical work on bile acids, sterols, steroid hormones, and their metabolism is also excellent, in spite of the fact that some of the best papers on this subject have not been included. The article on "The Biochemistry of Malignant Tissue," by D. Burk and R. J. Winzler, can be recommended not only for its organization, but also for the vast amount of information which it summarizes. They have selected 621 papers from the more than 2000 recent original papers in this field for discussion in the space of 26 pages. Of special interest to biologists is the contribution of D. Glick on "Histochemistry." This deals with the histochemical identification and determination of some of the vitamins, enzymes, and hormones. It also includes some work on micromethods such as Cartesian diver micromanometric metabolism studies, electron microscopy, and high-speed centrifugation.

FRANK H. J. FIGGE

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ADVANCES IN ENZYMOLOGY *and Related Subjects of Biochemistry. Volume IV.*

Edited by F. F. Nord and C. H. Werkman. Interscience Publishers, New York. $5.50. viii + 332 pp. 1944.

The interrelationships of chemistry and biology are apparent in this volume. However, one wonders in reading it whether the cooperation and interchange of ideas in these fields is as close as it should be. *Advances in Enzymology* consists essentially of the views of a group of biochemists on the problems of biology and medicine. There is apparently no attempt to restrict speculation or to standardize the papers. There is thus considerable variation in the contributions and each must be evaluated separately.

An example of a speculative contribution is that of Gulick on "The Chemical Formulation of Gene Structure and Gene Action." It is clear that in the field of genetics, the biologist has forged far ahead of the chemist. This article is an attempt on the part of a chemist to bridge the gap. One must agree with the comment at the end of the article "that the direct and explicit aid rendered by chemistry to the understanding of genetics and biological evolution has been rather limited, though with the promise of more to come; but that aid by way of supplying patterns of thought and pertinent analogies has already become very important." It is a thought-provoking article.

The contributions of Pigman on glycosidases and of Herbst on "The Transamination Reaction" are critical and thorough. The chemistry of tyrosinase has been ably and clearly discussed by Nelson and Dawson. It apparent from the clear, convincing discussion that the authors have worked in this field for many years and have a thorough knowledge of the chemistry of this enzyme. It is, therefore, appropriate for the review to be limited to the chemistry of the enzyme or the *in vitro* experiments of the authors and a few other workers. Even a speculative attempt to correlate these purely chemical data with some of the *in vivo* work on pigment formation would have made this a more valuable and comprehensive review for biologists. It is regrettable that biologists and chemists, in this field of natural pigments, have a tendency to travel in separate spheres.

The review of Hotchkiss on "Gramicidin, Tyrocidine, and Tyrothricin," the substances derived from bacteria that have antibacterial activity, is timely. It includes much that is fundamental in the field of bacterial physiology; some of this may find application in studies on the mechanism of action of other chemotherapeutic agents.

The discussion of "Biological Energy Transformations and the Cancer Problem" is an attempt to link the etiology of cancer to the conversion of a non-specific enzyme x into a "cancer virus." Just as other theories on the etiology of cancer, this is somewhat speculative. It contains much information on the enzymology of normal and malignant cells.

The chapter on "The Influence of Hormones on Enzymatic Reactions" is conspicuous for its brevity. The meagre amount of existing knowledge which has been included indicates that investigation in this important field has been neglected. The search of the literature has not been too exhaustive, however, as the influence of sex hormones on serum acid phosphatase and on tyrosinase were not mentioned.

The section on "The Absorption Spectra of Vitamins, Hormones, and Enzymes" is a concise and informative discussion. One very valuable feature is the inclusion of many graphs of characteristic absorption spectra of vitamins, hormones, and enzymes.

FRANK H. J. FIGGE

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THE CHEMISTRY AND TECHNOLOGY OF FOOD AND FOOD PRODUCTS. *Volume I.*

Edited by Morris B. Jacobs. Interscience Publishers, Inc., New York. Both volumes, $19.00; singly, $10.50. xv + 952 pp. 1944.

This is the first volume of an exhaustive treatment of the chemistry and technology of food. The forty-one contributors to the two volumes have made an ambitious and successful attempt to prepare a unified, authoritative account of the various phases of the subject from the point of view of specialists in these fields. The list of contributors, therefore, includes food technologists, chemists, physicists, biochemists, bacteriologists, pharmacologists, sanitary engineers, food inspectors, and entomologists. The twenty-three chapters in the first volume were written by twenty-one collaborators.

The first eleven chapters, on fundamentals, deal with the aspects of food chemistry that are common to all foods. Physical chemistry, carbohydrates, lipids, amino acids, proteins, enzymes, vitamins, hormones, minerals, digestion, and fate of food-stuffs comprise the main chapter headings in this section. It is a complete, yet concise coverage of the chemical aspects of food. If this part of the book were to be published separately, it could, with minor additions, serve as a textbook of physiological chemistry for colleges. The physiological coverage, which is of secondary interest, is not as complete as the chemical.

Some of the chapters on the section on fundamentals of food chemistry are applicable to other biological specialties and are so well written that they deserve special comment. The chapter on the chemistry of amino acids and proteins is a remarkably well organized and clear presentation of the elementary facts and also includes the recent work in the field. The references to other reviews and to original work are numerous. The same may be said of the chapter on enzymes by Stern. This very clear, concise, and up-to-date account can be recommended to the biologist who wishes to either review or become acquainted with the fundamentals of enzyme chemistry. The discussion of vitamins in the chapter on vitamins, vitagens, and hormones, appears to be an abstract of the author's very excellent book on this subject. For many, this discerning condensation will perhaps be advantageous.

A more complete discussion, or perhaps a special chapter, on the symptoms resulting from deficiency of various food substances could have been included in a comprehensive work of this kind. Perhaps this will appear in the second volume. The supplementation of foods and food products with vitamins and minerals could also have been placed in this part on general fundamental food chemistry, perhaps as a special chapter. Omissions as well as duplications, while unavoidable in such a collaborative effort, are rare. However, the addition of iodine to salt as a goiter preventive is not mentioned in the discussion of either iodine or salt as food factors. The enrichment of flour is fully discussed in the chapter on cereal grains; and the fortification of milk and milk products is briefly mentioned.

In the second part, an organized account of all the basic types of foods is presented. In most of the chapters in this section, an account of the history, definitions, standards, composition, and chemistry of the various basic foods are given. The data were collected from widely scattered sources in the scientific and technical literature, and numerical values have been condensed in the 179 tables included in this section. The subject index of 50 pages appears to be adequate and facilitates the use of this volume as a reference book, for which purpose it was intended.

Frank H. J. Figge

Soybean Chemistry and Technology.

By Klare S. Markley and Warren H. Goss. Chemical Publishing Company, Inc., Brooklyn. $3.50. vii + 261 pp. 1944.

This is a timely book on the chemical and technical aspects of the versatile soybean whose industrial and food uses are rapidly expanding. It is a summary of the numerous research contributions and references that have appeared in the literature up until 1943. One of the authors is a soybean chemist and the other is a chemical engineer; both have been active in the research field covered by the book, which appears to be authoritative, thorough, and complete. The book will be welcomed by those working in the field, for it is a well organized and clear presentation of a large amount of factual information. Biologists and biochemists working in the fields of edible oils and the vitamin and protein supplementation of foods will find the book useful.

Part I, which deals with the chemistry and physical properties of soybeans and soybean oils, covers phosphatides, antioxidants, and vitamins at greatest length. Proteins, enzymes, carbohydrates, glycosides, pigments, and sterols are also discussed. Part II reviews the historical development of soybean processing. It also describes in detail the most up-to-date methods and machinery for processing, extracting, and refining soybean products. Finally, there is a discussion of the processing of soybean oil for food uses. The more recent developments in the use of soybean products in plastics and possible industrial uses were not included.

Frank H. J. Figge

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The Constituents of Wheat and Wheat Products. *American Chemical Society Monograph Series Number 96.*

By C. H. Bailey. Reinhold Publishing Corporation, New York. $6.50. 332 pp. 1944.

This monograph is a compilation of the existent literature dealing with wheat and the substances that it contains. The first chapter relates the early researches on wheat proteins and includes a table showing the flour protein nomenclature arranged chronologically from 1728 to 1904. Chapters on prolamines, glutelins, water and salt soluble protein, crude protein, and crude glutein follow. These chapters contain summarized accounts of the various methods of hydrolysis and extraction of these substances, methods for the determination of the proteins, methods for the determination of the molecular weights of the protein, and methods for the determination of the products of hydrolysis of the wheat protein. There is also included in the chapter on crude protein and crude glutein a discussion of the variation of protein content in wheat grown over a wide range of territory that exhibits a great range of soil types and climatic conditions. Tables and distribution curves help to clarify this information.

The other chapters discuss nucleic acid, non-protein nitrogen, starch, sugars, other carbohydrates, lipids, minerals, halogens, sulfur and selenium, acidity, pigments and vitamins of wheat and wheat products. These chapters also contain summaries of the original literature. They are concise and tables are quoted that help also to summarize the information. The author of the monograph comments on the various reports and points out conflicting ideas in the literature. The chapters are well organized, each beginning with a brief historical introduction. At the bottom of each page one finds the references to the original literature cited on that page.

This monograph is of great value to anyone interested in wheat and its constituents. It gives excellent, concise information for the technical worker and abundant references for those who want more detailed information.

MARGUERITE M. SCHMIDT

WOOD CHEMISTRY.

Edited by Louis E. Wise. Reinhold Publishing Corporation, New York. $11.50. x + 900 pp. 1944.

This book is a successor to *The Chemistry of Wood* (1926), by L. F. Hawley and L. E. Wise, Monograph No. 28 in the American Chemical Society Series of Scientific and Technologic Monographs. It represents an expansion in scope as well as a modernized treatment of the subject matter. It is a compendium written by thirteen authors, each contributing one or several chapters on his own field of specialization. It is divided into six parts, as follows:

I. The Growth, Anatomy and Physical Properties of Wood.
II. Components and Chemistry of the Cell Wall.
III. The Extraneous Substances.
IV. Surface Properties of Cellulosic Materials.
V. The Chemical Analysis of Wood.
VI. Wood as an Industrial Raw Material.

Emphasis is placed on recent research on various phases of wood chemistry and related fields. The treatment is not general but is one of selected topics which are thoroughly covered, with respect to basic information and principles, technique, and evaluation of needs and trends of future work. Of particular interest to the biologist, as well as to the workers in the numerous specialized branches of wood technology, are several chapters on borderline fields, such as an extensive treatment of the structure of plant cells that includes aspects of growth and morphology; a discussion of "plant cellulose" vs. true cellulose; the chapters on surface properties and colloidal behavior; and the last, timely chapters on the decomposition of wood by microorganisms.

FOLKE SKOOG

PSYCHOLOGY AND ANIMAL BEHAVIOR

PSYCHOLOGY IN LIVING.

By Wendell White. The Macmillan Company, New York. $2.50. x + 333 pp. 1944.

This book, by the author of *Psychology of Dealing with People* and of *Psychology of Making Life Interesting*, contains the substance of these two earlier books. It was prepared with the assistance of evening-school students of the University of Minnesota, to whom preliminary drafts were given in mimeographed form. It has, therefore, grown out of a very practical situation, one which demands that materials be presented in nontechnical everyday language.

We believe that the book must have met the specific needs admirably. It is stimulating, challenging, and interesting. And, though sufficiently full, it is concise, not being weighted down with wordy details of case studies which the formal textbook in mental hygiene usually has.

The book has two main divisions: Part I, "Psychology in Personal Relationships" (108 pp.), and Part II, "Psychology in the Achievement of Mental Health" (208 pp.). The chapter titles in Part I can be only barely suggestive of the materials and of the skill with which the author presents the different facets of behavior that may be grouped under the term "tact." This is one of the best presentations we have seen. Instead of presenting the usual case studies, the author weaves really practical materials, with a few sentences, into his context. The methods are often presented in a series of tactful, aphoristic statements. The chapters are: "Indirect Presentation of Ideas", "Direct Presentation of Ideas", "Inoffensive Opposition to Ideas", and "Misuse of Psychology." It is these chapters, especially, together with other chapters mentioned later, which distinguish this book from discussions only partially overlapping Dr. White's and from the more formal presentations in textbooks on mental hygiene, mental adjustments, or abnormal psychology.

Besides the chapters which deal with such usual topics in abnormal psychology as "Problems of Mental Health", "Unwholesome Adjustments", "Daydreaming", "Rationalization", "Extrusion of Thoughts from Consciousness," "Wished Physical Disabilities", and "Prevention of Unwholesome Adjustment", several of the remaining chapters are especially attractive as to content, treatment, and practical value. These are the chapters on "Pride-Sustaining Activity", "Freedom," and "Love." Besides these vital motives in human life, there are other strong ones, such as are indicated by the headings "Respectable Living and

Working Conditions", "Interesting Experiences", "Interesting Occupational Experiences", "Interesting Recreational Experiences", "Social Contacts", and "A Livelihood and Sense of Security." In the latter half of the book, Dr. White draws upon a number of relevant objective studies.

A set of "Self-testing Exercises" at the end, consisting of 133 statements quoted from the book, is presented by the author for the reader to use in trying to recall what was indicated in the text as well as elsewhere.

The author emphasizes the "constant need of our being versed in the science, and skilled in the art, of dealing with people. Competence in the directing or influencing other persons, and in managing one's own life, includes essentially an understanding of human nature." Strong though the "sense of personal worth" may be, the author points out that no one of the fundamental motives can be called "a master passion, since each in turn may swallow the others." "Other motives may (and do) in alternation take precedence over this one."

This book is one to be recommended to the general reader for his own self-improvement, as well as to teachers of classes on practical psychology and mental hygiene. The author's invigorating spirit is bound to be transmitted to others, and especially to those who need most to understand their own motives and maladjustments, and to learn how to make such adjustments most sensibly to the needs and requirements of their household and society.

C. Hart Westbrook

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PRACTICAL PSYCHOLOGY.

By F. K. Berrien. The Macmillan Company, New York. $4.00. xii + 584 pp. 1944.

"The author's aim throughout this text," he writes, "has been to survey the chief problems in which the applied psychologist has made some contribution"; "to present sufficient background information for the reader to understand, first, the significance of the problem, and second, the broad principles upon which the psychologist's contribution is based." The experimental studies summarized in the text (and there are enough of them to give a good picture, without so many as to weary or annoy the average serious reader) were selected "largely because of the degree to which they represented 'field' as contrasted with 'laboratory research,' even though a field study may only verify a conclusion previously established more accurately in a laboratory." The author believes that many previous texts in this field have "lacked a realistic tone because of their emphasis upon pedantic-appearing laboratory investigations, and, secondly, the student and the layman are more readily convinced of many propositions by reference to studies made outside the highly controlled conditions of academic laboratories." He also thinks the layman and the student (perhaps, better, the *beginning* psychology student) are "more interested first in conclusions and, second, in the evidence and procedures upon which these conclusions are developed." For these reasons the book has been written primarily for those with little or no previous contact with the usual elementary psychology course. Except for the chapters on "Study Efficiency," "Psychology and Learning," and perhaps those on "Principles of Mental Hygiene," "Mental Hygiene and Guidance," and "Vocational Guidance," this book has no more material in common with a present-day elementary psychology course than the occasional illustrations which the author of the general psychology might draw from findings in the various fields of applied psychology. For this reason and the aims stated by the author himself above, the text should prove to be an excellent introduction to "practical psychology" and should entice a thoughtful reader and student to follow up this introduction with a thorough course in general psychology, and, later, perhaps, more advanced work.

The chapter on "Adjustments in Old Age" adds much to the value of the book, for it comprises material which is only beginning to be treated in separate chapters in psychology books (except in books on developmental psychology) and to be given the prominence it requires, especially with the increasing proportion of older persons in our population. This chapter is very well done and will be both interesting, practical, and suggestive to those who themselves are in the period of "later maturity" (just before 60) as well as to those who have passed 60 and are classed by the author as "senescent." Then, too, there is much which should warn and guide the young person in his own preparation for old age, as well as give him a better understanding of, and consideration for, the older persons around him.

The style is smooth, readable, and interesting. Avoidance of technical terms, a generous provision of clear, attractive graphs and pictures, freedom from too many, too long, or unattractive tables, a good size of type and the excellent choice and organization of the material, all help to make the book one of the best we have seen for its purposes. It could well be used with adult education classes or evening classes for those who wish to follow up interesting leads and get practical everyday help rather than to earn 'credits' or work for degrees.

C. Hart Westbrook

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LIVING WITH CHILDREN.

By Gertrude E. Chittenden. The Macmillan Company, New York. $1.75. ix + 163 pp. 1944.

This comprehensive and graphic little volume might well be called a handbook or manual. It should appeal both to students and to parents. It deals with boys and girls from birth on through the college years. The characteristics of verious phases of growth and development and some reasons for behavior are considered. No one age group or phase is emphasized to the exclusion of another. For instance, the first chapter includes children of preschool, grade, and college age. Physical and physiological, mental, emotional, and social phases are given equal weight. Examples are described of a four-year-old boy, a grade school girl, a college freshman girl, a college boy-president of a dormitory,—all forming social patterns under their respective surroundings. The content of the book is thought-provoking, and in no place does the author dictate or impose her opinions. The text, with its excerpts from studies and books and its many graphic descriptions of children of different ages in a variety of everyday situations, helps the reader to form his own answers. Chittenden makes use of the works of well known and recognized authors and specialists in the fields of anthropology, psychology, child development, psychiatry, and sociology. A student of community hygiene and sociology should profit by this book, as should a student of child development. Parents will note that old theories and beliefs are not ignored but are questioned rationally, and more recent attitudes concerning the child's learning to walk, talk, sleep, and eat drive away old bugaboos and worries.

The author does not take a "holier than thou" attitude about our culture, as so many people are prone to do. Instead, she invites us to weigh our social patterns and compare them with those of the Samoan people studied by Margaret Mead. The reader will be reminded of the significance of the quotation—"All men are created equal"—when he reads, "There is a belief in our culture that any child, regardless of his capacities and limitations and of the difficulties he faces, can reach any goal that is set up for him. Needless to say, this belief is a fallacy, but the fact that it does exist probably accounts to a large extent for the American's great urge to be successful." The meaning of democracy flows through the text. It is not preached; principles are not theorized; instead sound facts are looked squarely in the face. No reader can fail to see the importance of the "family as a laboratory for democracy" or to be impressed with the responsibility of the home and community to the child.

The book deals with current problems arising from wartime conditions and the present-day interests of children in comics and radio. Nearly seven-eighths of the footnote references are dated between 1933 and 1943. The last chapter classifies books and pamphlets under such headings as prenatal care, children's clothing, and sex education. These latter forty-one references are well annotated and include the literature from 1932 to 1943. An average of four to five well selected references, ranging from 1937 to 1943, follow each of the first seven chapters. Many of the book's references, including those in the footnotes, are those undergraduates in courses in child development use. Subheadings are introduced by a paragraph that orients the reader for the discussion to follow, and a simple, concise summary comes at the end of each chapter.

CLAIRE QUINCER

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THE BRUSH FOUNDATION STUDY OF CHILD GROWTH AND DEVELOPMENT. I. PSYCHOMETRIC TESTS. *Monographs of the Society for Research in Child Development Volume VIII, Number 2 (Serial Number 35).*

By Elizabeth Ebert and Katherine Simmons. Society for Research in Child Development, National Research Council, Washington. $1.50 (paper). xiv + 113 pp. 1943.

This monograph represents the psychometric fruits of the eleven-year Brush Foundation study of the growth and development of a large number of Cleveland children. The main results are based upon longitudinal studies of a sampling of superior children. The work has been painstaking, with hardly a detail unturned that might yield a possible relationship. The results include comparisons between the 1916 and 1917 Stanford-Binet scales, between these scales and several performance tests, data on sex differences, on the validity of the Otis group tests, on various test-retest coefficients; they furnish further data on losses and gains in I.Q., add to the accumulating evidence concerning the relative effectiveness of preschool tests in the prediction of later standing, and to the evidence concerning the apparently genuine changes among some children in the rate or tempo of mental growth. In the light of the recent interest in using terminal status as one of the criteria for the selection of test items, the data are interesting that show correlations between previous test scores (Binet and performance) and standing on Progressive Achievement batteries in the junior and senior high school grades.

The work of these investigators in straightforward reporting of statistical relationships is valuable in this period of a renewed critique of mental tests. It is unfortunate, however, that they failed to use the concentrated insight that this large study must have given them, either to put their own results into a clearer perspective or to project with vision the problems for the future raised by their own work and that of others!

THETA WOLF

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PERSISTENCE AND CHANGE IN PERSONALITY PATTERNS. *Monographs of the Society for Research in Child Development, Volume 8, No. 3 (Serial No. 36).*

By Katherine Elliott Roberts and Virginia Van Dyne Fleming. Society for Research in Child Development, National Research Council, Washington, D. C. $1.50 (paper). vii + 206 pp. 1943.

This monograph is an attempt to study the personality development of college women in three of their life stages ("pre-college," "college," "post-college") in order to determine qualitatively and quantitatively the persistence and fluctuation of their personality patterns. It is based upon twenty-five extensive case studies from the files of the Merrill-Palmer Advisory Service for College Women, and utilizes excerpts from these voluminous life-histories as primary material for analysis.

The authors proclaim their belief in a dynamic, integrative concept of personality, but their procedure results in an atomistic description that precludes any such personality. They have created 523 attitudes and 229 traits (sic!) by which they pretend to classify personality, and then proceed arbitrarily to impose this "system" upon their material. The evidence is discovered from a case history in which the subject herself was the witness for it, and evidence applicable to the present study was not asked for according to any organized plan. One finds it difficult, too, to accept the authors' distinction between their "traits" and "attitudes." For example: if a person "lets children solve their own problems," she exhibits an attitude; if the same person "tries to solve problems rather than avoid them," she exhibits a trait. Moreover, in making distinctions *within* the traits, the authors place in *separate* categories such subjective terms as "excitable," "explosive," "impulsive." A kind of behavior, then, might be labelled "explosive" at one "life stage" and very conceivably be called "impulsive" at another stage, with results indicating fluctuation in pattern; a different labelling would, on the other hand, have shown persistence. Furthermore, if this kind of behavior did not happen to appear again *in the case history*—at another life stage—the results were treated as though the behavior did not occur, although it is clear that it simply may not have been reported. This fact irreparably and unaccountably affects the results.

Again, in the case histories, a false picture of persistence or of fluctuation is given because the setting of the behavior—or its meaning to the individual—had to be ignored. A person who may always be "sensitive" in a given social situation might conceivably "persist" in this behavior throughout the three stages, but in accordance with the plan in this study, because she was sensitive in situations x and y, and *not* sensitive in situations a and c, the "trait" is tabulated as fluctuating.

These conscientious authors very evidently wished to draw some important educational lessons from this study. It is regrettable that so much honest work was spent upon such an unproductive project. The material might have been studied from the point of view of integrated personality. A fair sampling of the case histories, analysed and briefed in a non-statistical manner, could have given evidence both of the persistence and modifiability of human behavior that was colorful, dramatic, and useful. On the other hand, it is abortive to attempt to force into statistical units material collected without method, without defined aim or uniformity, and replete with gaps that, if filled, might have changed the results altogether.

THETA WOLF

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THE MEASUREMENT OF ADULT INTELLIGENCE. *Third Edition.*

By David Wechsler. The Williams & Wilkins Company, Baltimore. $3.50. vii + 258 pp. 1944.

In this third edition, the author's aim has been "to increase the book's usefulness to those engaged in the field of applied psychometrics." He has in mind particularly the military applications of the Wechsler-Bellevue Scale, now being used by some of the armed services of Great Britain as well as by those of the United States. The numbers and titles of the chapters have not been changed from those of the second edition; but chapters 6 and 11 have been "somewhat extended and in part rewritten," and contain most of the changes that have been made.

One outstanding value of the Bellevue Scale is that it enables clinicians to measure and score separately by the Verbal and the Performance Scales the two distinct groups of abilities or capacities, verbal and performance, which in some other widely used tests are measured by a single scale and indicated by a composite score. This composite score has concealed certain significant deficiencies and has thereby tended to mislead those who have accepted and dealt only with the final result, the figures for M.A.'s and I.Q.'s.

Another value of the book is that the extension of the Scale to mental levels higher than those measured by any other but Thorndike's CAVD Scales makes possible the mental measurement of persons up to the age of 60 years, and by a process of extrapolation, "without serious error by the use of some simple multipliers which take care of the age factor," of those between 60 and 80 years.

In this latest edition, moreover, Wechsler has completely revised the table of "signs" for different clinical entities revealed by the tests and has elaborated a new quantitative method for the determination of mental deterioration. These changes will render the book much more valuable to the clinician, both for his own records and in his interpretation of the results for the guidance of other members of the clinic in their final diagnosis and in the treatment and disposition of difficult cases. Alterations in the scoring of certain subtests and in the use of scores of subtests for further analysis of the mental deterioration or improvement of the subject constitute another improvement in the Scale. Further, the I.Q. range at the upper end of the Scale has been increased, "without, however, altering significantly the norms for the population as a whole."

Chapter 11, on Diagnostic and Clinical Features, should be especially valuable, as it contains tables of test characteristics of the clinical groups, followed by comments on the groups and illustrative cases, each accompanied by a tabulation of the scores made on the subtests of both Verbal and Performance scales and the respective I.Q.'s.

In the standardization of the Bellevue Scale, the author found the following correlations with his criteria for validity: (1) Bellevue I.Q.'s and Stanford-Binet I.Q.'s: r = .82 ± .026; (2) with judges' (teachers') ratings, r = .43 and .52; (3) with psychiatrists' ratings of "recommended" or "not recommended" to commitment to a state institution for mental defectives, r = .79 ± .048 (in contrast with Binet I.Q.'s, where r = .33 ± .071). High correlations, empirically, existed with clinical criteria, such as: (1) social history; (2) comparative efficiency in verbal and performance tests, and in the latter versus vocational aptitude, motility, and ability to adjust to unfamiliar patterns of life; and (3) differentiation of general intelligence from educational disabilities. Of the 5000 subjects tested, only 3000 were used for the stanardization.

For three of the four measures of reliability generally used, the author got the following results: (1) S.E. of measurement for the Full Scale (I.Q.'s), whose mean and S.D. are, respectively, 100.11 and 14.69, is 5.674; (2) degree of correlation between the various portions of the same scale, 4 subtests x 4 subtests, r = .90 ± .014, and between verbal I.Q.'s x Performance I.Q.'s, r = .83 ± .018; (3) correlations between retests with the same subjects, children's r = .94 ± .013, adults' r = .94 ± .018.

In addition, correlations found by other investigators of the Full Scale with Stanford-Binet (1916 Revision) for various groups are: .57 ± .04, .81 ± .03, and .82 ± .03; with S-B, 1937 Rev., L, are .62 ± .04, .89 ± .01, .91 ± .02, and .93 ± .01. The two lowest r's, .57 and .62, are for college freshmen, both sexes combined and females, respectively. The remainder are for mental patients, (.89, .91, and .93), and for adolescent male delinquents, and adolescents aged 12–16.

In eight other studies, including the use of six different group tests of intelligence, the Bellevue Scale correlated from .39 ± .07 to .81 ± .04. Still other studies show correlations of various tests with the Bellevue Verbal Scale ranging from .48 to .92. Correlations of the Performance Scale with other scales are systematically, and often markedly, lower, than those of the Full Scale with other scales.

In view of the well adapted materials used and the evidences of standardization, validity, and reliability presented by the author, it seems that the new edition of the Bellevue Scale should prove to be highly reliable and valid for general use as well as for the special use intended with returning soldiers in the problems of their rehabilitation.

C. HART WESTBROOK

FEAR IN BATTLE. *Fighting Forces Series.*
By John Dollard, with the assistance of Donald Horton. The Infantry Journal, Washington. 25 cents (paper). v + 64 pp. 1944.

"This study of fear and courage under battle conditions is indebted first of all to 300 veterans of the Abraham Lincoln Brigade (volunteers for the service in the Civil War in Spain). . . . " "This group varied as to age, region, social status and political conviction. They had in common the belief that by volunteering they were fighting for democracy. Different as they may have been from a cross-section of the American army," they were hardened soldiers and had much in common. Their testimony "seems sensible and soldierly." "The typical informant was a rifleman, non-commissioned, poorly trained by American Army standards, wounded. All observers seem to agree that he was a tough fighting man." "The study bears only on the military experience of the informants. . . . "

The several parts of the study deal with: Some Facts about Fear; Changes in Fear; Techniques of Fear Control; Fear and Morale; and Facts about the Report, including reliability, validity, errors of report, cause and identification with cause, and unconscious fear. The "Findings in Brief" are presented in 20 statements. These cannot be stated here for lack of space.

Each part is presented in a number of sections made up of summaries or generalized statements and occupying one page each; opposite each such page of facts or generalizations is an adequate graph of the percentages of the various statements.

The booklet will be of special interest to the psychologist as a study of one of the emotions, and should be of practical value to officers whose duty it is to train soldiers in the homeland or for service abroad. Perhaps it will be of most immediate value to officers and the men of the ranks themselves in the war areas of the world before, during, and after battle.

This study has blazed the path. Others should be carefully planned and pre-battle attitudes and fears discovered before the men go abroad; then continued with the men overseas, and, finally, carried to completion with men when they return on furlough and after they are discharged. The psychologists connected with the services, both at home and abroad, could do a fine piece of service in this way, calling in civilian psychologists to share the task with them here.

This is a very clear, interesting study of practical value, and it should stimulate much more research on the subject.

C. HART WESTBROOK

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PSYCHOSOMATIC MEDICINE.
WAR PSYCHIATRY.
PSYCHOTHERAPY FOR CHILDREN. GROUP PSYCHOTHERAPY.

Proceedings of the Second Brief Psychotherapy Council, Chicago, Illinois, January, 1944. Institute for Psychoanalysis, Chicago. 75 cents each; $2.00 a set (paper). 55 pp.; 64 pp.; 58 pp. 1944.

In the first of these three little volumes of proceedings, *Psychosomatic Medicine*, Alexander outlines the purposes and outlook of the Brief Psychotherapy Council. He defines the function of the Council as the bringing together of different investigators in order to afford an opportunity for exchange of views and experiences. He denies any rigidity of spirit in the organization, and while the Council operates under the Chicago Institute for Psychoanalysis, "it is no more representative of psychoanalysis than of group psychotherapy, psychodrama, hypnosis or narcosynthesis."

The contents of these volumes would give considerable support to this breadth of view. For example, the volume *Psychosomatic Medicine* contains an article by Barach on "Impairment in Emotional Control Produced Both by Lowering and Raising the Oxygen Pressure in the Atmosphere." Essentially a matter of research inspired by physiology, this contrasts with an article by Thomas M. French, "Brief Psychotherapy in Bronchial Asthma," which gives a beautifully stated summary of a case treated by Adelaide Johnson through analytic procedure with excellent results. Franz Alexander's study of hypoglycemic fatigue combines the physiologic and psychologic attacks on the problem. Weiss' paper on "Psychotherapy in Psychosomatic Disorders of the Gastro-intestinal Tract," and Daniels' on diabetes mellitus conclude this volume full of vivid experience vividly told.

The volume on *War Psychiatry* is equally good. A measure of the diversity of the attack on this matter is illustrated by the following titles: "Some Special Aspects of Psychotherapy in the Army Air Forces," by Murray; "Brief Psychotherapy in War Neuroses," by Grinker; "The Cornell Selectee Index," by Mittelmann; "Brief Psychotherapy in the Merchant Marine," by Blain; "The Use of the Multiple Choice Test (Rorschach) in the Military Services," by Harrower-Erickson. There is no particular point in singling out any one of these articles for special mention, since all are excellent. Grinker's statement concerning the war neuroses was very forcefully presented. Rado, in discussing Grinker's paper, pointed out that narcoanalysis had been used extensively in the last war, and that digestion of the traumatic experience even with this method does not guarantee the victim against recurrent difficulty. Rado claims that this can only be done by desensitizing the victim to trauma and training him in the psychological technique of handling himself in combat. He also pointed out that in World War I war neuroses, with a somewhat different symptomatology, it is true, were relieved much more quickly in large numbers by faradic shock in a proper atmosphere of suggestion.

In the third volume, divided into two parts, *Psychotherapy for Children* and *Group Psychotherapy*, there appear some very interesting papers. In the first part are Marian C. Putnam's description of "Psychotherapy in a Guidance Center for Infants and Pre-School Children"; Editha Sterba's "Brief Psychotherapy with Orthopedic Cases"; Liss' "Thrombocytopenic Purpura in a Case of Sado-masochism"; and Emmy Sylvester's "Emergency Psychotherapy of Pathologically Severe Feeding Disturbances in Children." This last paper may be singled out as an example of the shrewd use of intuition in dealing with what is always an exceedingly trying problem. The author states in detail exactly how she managed to develop rapport with a certain severely disturbed child and to achieve a resolution of the problem. This will well repay careful reading. In the second part, Redl describes the "Problems of Clinical Group Work with Children"; Lewis, "The Solution of a Chronic Conflict in Industry"; and Moreno, "A Case of Paranoia Treated Through Psychodrama."

These little booklets show that a great deal of effort is being made everywhere to break down the tremendous waste of time inherent in most methods of psychotherapy, a goal which one can only devoutly hope will be advanced along technically unassailable lines. When Alexander points out that a single contact with a patient may often produce as much good as a protracted analysis, he is only stating what the experienced psychiatrist has known for a long time. The question is how to organize information concerning pathology and therapy so that this goal can be more often reached.

WENDELL MUNCIE

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CASE STUDIES IN THE PSYCHOPATHOLOGY OF CRIME. *A Reference Source for Research in Criminal Material. Volume Two.*

By Ben Karpman. Medical Science Press, Washington. $16.00. viii + 738 pp. 1944.

In this volume of some 738 pages Karpman has dragged out in detail the material, a considerable portion of which is autobiographical, on four criminals, the first convicted of theft of the U. S. mail and of drug addiction, the second of violation of the Mann Act, the third of rape, and the fourth of mail train robbery. This volume, in contrast to volume I of the series, has included some sexual crimes, whereas volume I dealt entirely with predatory crimes, and volume III, projected, is to deal with murder exclusively. This volume gives a great deal of material as the free association coming to light in psychoanalytic sessions, and one case, the second one, benefitted from the therapy through the discovery of a neurotic compulsive factor.

There may be some reasons which escape one for so extensive a presentation of such case material, but unfortunately it seems only long, tedious, and repetitious, with no special merit because it is in the victims' own words. It seems that a much more effective presentation would have been to give a concise statement of the case and extracts of the critical moments in treatment couched in the patient's and the physician's own words. It is hard to believe that the careful, conscientious reading of any one of these four case histories will add very much to the knowledge of causes, course, and treatment of criminality in general. The first volume was likewise overburdened with words, with a dearth of concise lessons to be learned from it. The one case in the present group, number two, which profited by psychotherapy is rather interesting from that standpoint alone. The perusal of the case history also shows that there was a great deal of wasted effort and time in the psychoanalysis, and one may wonder if the same material might not have been discovered with the same advantageous consequences to the patient by much simpler means. To put it briefly, this pretentious volume leaves one unconvinced of either the necessity for this kind of presentation or of any special results likely to accrue from it.

WENDELL MUNCIE

HUMAN BIOLOGY

STUDIES IN THE ANTHROPOLOGY OF OCEANIA AND ASIA *Presented in Memory of Roland Burrage Dixon. Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XX.* *Edited by Carleton S. Coon and James M. Andrews, IV. Published by the Museum, Cambridge, Mass.* $6.00 (cloth), $4.50 (paper). xiv + 220 pp.; 20 plates. 1943.

This collection of fourteen anthropological studies is presented in memory of Roland Burrage Dixon by a group of his former students. Dixon was Professor of Anthropology at Harvard University from 1915 to his death in 1934. The volume opens with a brief biographic sketch of Dixon and a complete bibliography of his works. Nine of the contributions to this volume are devoted to ethnological and archeological subjects, namely: Polynesian Stone Remains, by K. P. Emory; Petroglyphs in the Marquesas, by E. S. C. Handy; Gods of Rennell Island, by G. MacGregor; Some Aspects of Religion in Bougainville, by D. L. Oliver; Australian Totemism, by R. L. Sharp; Culture Sequences in Madagascar, by R. Linton; Certain Ancient Burial Customs and Mortuary Objects from China, by L. Chi; Observations on the Bronze Age in the Yenisei Valley of Siberia, by J. H. Gaul; and a review of all available information regarding the Prehistory, Archaeology and Ethnography of Southern Arabia, by C. S. Coon.

The remaining five papers deal with problems of physical anthropology and as such are of particular interest to biologists. The first of these studies, by H. L. Shapiro, bears the title "Physical Differentiation in Polynesia," and leads to the following main conclusions: The Polynesian population shows a basic unity in its physical type and seems to have been derived from a fairly homogeneous ancestral stock in an as yet unknown area, which sent out successive and chronologically widely separated waves of invaders to all parts of Polynesia. The detailed physical differences among the present-day inhabitants of Polynesian islands may be due partly to local inbreeding or, more commonly, to the gradual differentiation in the original stock during the long period of emigration.

In another contribution, W. W. Howells discusses the Racial Elements of Melanesia, on the basis of our still very meagre knowledge of the physical anthropology of this region. Howells suggests that the first comers to Melanesia were Australian aborigines who had reached New Guinea, the Bismarck Archipelago, New Caledonia, and possibly a few other islands. The next immigrants were Negritos, who mixed with the Australians in New Guinea, but replaced them in New Britain, the Solomons, and the New Hebrides. The following arrivals, who probably came in many and long-continued invasions, were Negro peoples "resembling the typical Congo forest stock." These settled the lowlands of New Guinea, interbreeding with their predecessors, and extending their domain gradually to many of the other islands. Micronesian and Polynesian intrusions became superimposed later on and further complicated the racial composition of these regions.

In a paper on "Linguistic and Racial Aspects of the Munda Problem," G. T. Bowels reviews the information and theories concerning those isolated human groups in northern India who speak Munda languages, and he contributes many new observations on the physical characters of these people. The latter form a valuable and rare record; they are based on extensive series of individuals and contain accurate data for the most significant body measurements as well as for nonmetric features.

J. M. Andrews, IV, in an interesting essay on Evolutionary Trends in Body Build, makes use of his great collection of anthropological measurements on Siamese, as well as of certain findings by some other authors, to demonstrate lasting changes in human physique apparently resulting from environmental stimuli. In Siamese, Japanese immigrants of Hawaii, and New Englanders, who have changed their environmental conditions during one or more generations, body form has become altered in a strikingly similar manner. They have all acquired a greater stature and proportionately greater weight, and in addition there has occurred an increase in *relative* limb lengths and in *relative* shoulder and chest diameters, and a decrease in *relative* chest depth and hip breadth.

"Physical Types Among the Japanese" is the title of a paper by F. S. Hulse. Historical and ethnological sources can tell us very little about the racial background of the Japanese, and archeological material, dating at most to the Neolithic period, is for Japan still scarce and inconclusive. The evidence uncovered so far indicates that the ancient inhabitants of the Japanese archipelago "apparently belonged to a branch of mankind sharing characteristics similar to those of the Australoid and to those of the Caucasian. This is also true of the living Ainu." After reviewing our inadequate knowledge of the physical anthropology of the recent Japanese population, the author presents some very welcome new data showing the morphological characters of living Japanese. Among the various existing types one can recognize some obviously pre-Mongoloid elements as well as those which lack Australoid or Caucasian features. Still other types possess in some respects a remarkable similarity to certain Chinese.

With these many notable studies on a wide variety of problems this memorial volume forms a very valuable addition to every anthropological library.

Adolph H. Schultz

CHINA. *Smithsonian Institution War Background Studies Number Twenty.*

By A. G. Wenley and John A. Pope. Smithsonian Institution, Washington. 25 cents (paper). v + 85 pp. 1944.

This brief introduction to China is comprehensive and enlightening to a degree hard to believe attainable within a mere 85 pages. The first main section, on China's geography, follows Cressey on the whole, and concisely discusses the topography, climate, soil, agriculture, mineral resources, and populations of the land, region by region. Some of the figures for the populations of cities are not the most recent, and some are perhaps not good estimates at all, but sufficient warning is given about the unreliability of statistics on China. Wenley gives in eight pages a most illuminating account of the Chinese language, an account that could hardly be bettered in so brief a compass. Pope takes up China's history and foreign contacts, supplemented by an account by Wenley of China's part in the present war. Social organization and government are discussed by Wenley, with proper definition of the Chinese family and due emphasis upon its place in Chinese life. The section on Chinese art is especially good, as one would expect from members of the staff of the Freer Gallery. Pottery and porcelain, calligraphy and painting, bronze and other sorts of metal-working, and sculpture, together with minor arts and music all receive consideration. The final section, on the Chinese mind, is by Pope. Here Chinese philosophy, religion, and science are outlined, revealing, on the one hand, the great significance of tradition in the Chinese mind, and on the other, their genius for accepting foreign ideas and influences and amalgamating them with the older patterns of Chinese thought.

There is a brief, well-chosen bibliography but no index. Three useful charts of the periods and dynasties of Chinese history complete the pamphlet. The twenty-five plates of photographs are exceedingly good; and the seven maps, although lacking detail, are fairly helpful.

This little volume deserves the widest circulation among American citizens. It might very well, with others of the same series, serve as material for a new type of course in our high schools and colleges.

Bentley Glass

PEOPLES OF SOUTHEAST ASIA.

By Bruno Lasker. Prepared under the auspices of the American Council of the Institute of Pacific Relations. Alfred A. Knopf, New York. $3.00. viii + 288 + x pp. 1944.

"The old relations between East and West were already in flux; crude exploitation and brute force have given way to principles of trusteeship, or guardianship, and of voluntary co-operation. The progressive application of these principles has been interrupted by the war. Now, the campaign of reconquest and the re-establishment of orderly rule provide a unique historical occasion. Here is the chance, in one of the world's most important culture areas, to do something more than just continue where we left off." In the pages that follow this introductory statement, the author discusses the problems, injustices, and general unrest that exist within the region, and demonstrates the need of a concerted effort on the part of the rest of the world to do something to alleviate the underlying causes. The fundamental aim of this book is to furnish the reader with authoritative information on existing conditions in order that he might more intelligently deal with these problems.

This region of islands, peninsulas, seas, swamps, and fertile soil is the home of an estimated one-fifteenth of the world's population. The native inhabitants belong to a wide variety of social groups ranging from headhunters to skilled artisans and cultivators of commercial crops. The author does much to dispel the general belief that these peoples of the Asiatic tropics are fundamentally inferior. Their apparent laziness and their willingness to use outmoded methods of agriculture is explained on the basis that they have not been convinced that greater industry and agricultural output furnishes adequate reward. Their lack of thriftiness is accredited to the fact that it is to the interest of certain groups that they fall into debt. We are reminded that these tropics have given the world some of the oldest civilizations. As evidence the author mentions the lofty and intricate Hindu structures recently discovered in Cambodia and Java, the Polynesian seafarers who conquered great distances in the Pacific long before Columbus succeeded in crossing the Atlantic, and the Malay and Arab mariners that linked China and Imperial Rome in trade. The inventiveness of the natives is also emphasized, and we are told that it was the Malay who taught us how to build the suspension bridge. The reader is shown that the region and the inhabitants have inherent potentialities that, if given opportunity and proper guidance, are capable of contributing much to civilization today.

In spite of the evils of the colonial system that has exploited the region for foreign interests, it has accelerated the progressive advance from lower to higher levels of civilization. Unfortunately, in many instances this has only given them a glimpse of a better life that they are unable to attain, and tastes which they cannot gratify. Although the Netherlands' government has done far more than the British for their subjects, neither has done enough to assure the natives that their position is to improve fundamentally. This has caused a contagious "oppression psychosis" to spread throughout the region. The people are conscious of their poverty and the restrictions that make it impossible for them to obtain what they now desire. "We are told that, even though the native cannot buy the same degree of physical and mental efficiency as the Occidental, he is happier in his native civilization. An enthusiast of the simple life—for others—may even add that the native is happy in proportion to his lack of contact with Western life and his ignorance of its paraphernalia. There might be something to this—though I doubt it, as everybody must who knows the perils and fears of primitive life—yet those who use that argument do not in the least intend that the carriers of Occidental civilization should move out and leave the natives a free field." Since the Occidentals are not willing to "move out," it is important that they relieve the troubled conditions. The author believes this can be done by a gradual change to self-rule through education and training for leadership; by encouraging and developing native industries; and by improving the agricultural and economic systems. In other words, the mother countries and their representatives should serve as trustees in the development of Southeast Asia rather than exploit the region to their own advantage.

The book is not a particularly readable one. This may be due in part to the frequent use of long sentences that are held together with many commas, semicolons, and dashes. Nevertheless, it is well worth the time and effort for the valuable material that it presents.

M. M. BROOKE

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OLD ORAIBI. *A Study of the Hopi Indians of Third Mesa. Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XXII, Number One. By Mischa Titiev. Published by the Museum, Cambridge, Mass.* $4.50 (paper). xi + 277 pp.; 4 plates. 1944.

In the field studies that form the basis of this monograph, the author has concentrated on two aspects of Hopi culture: social organization, and ceremonialism. He discusses these two items in the first two parts of his excellent book, while a third part (miscellany) and an appendix contain, besides an important chapter on "the economic background," mainly additional material on ceremonialism. The author has always integrated his own findings into the considerable body of existing material dealing with Hopi and Pueblo culture.

Titiev's handling of the data on "Kinship and Social Organization" is particularly praiseworthy, all the more since kinship data, ever since the evolutionary approach was given up, have been rather dead-weight in so many anthropological monographs of the past. Titiev gives not only a more detailed and correct description of kinship data than his predecessors; he also uses the more modern functional approach of supplementing mere kinship nomenclature by data on the reciprocal behavior of kindred. In analysing the split of Old Oraibi in 1906 into three villages, he shows the inherent tendency of Hopi social organization towards such developments, and is thus able to throw new light on the old and puzzling question why the Pueblo archeologist finds so many abandoned village sites. When Titiev reduces the three old explanations of this phenomenon —war, climate, and disease—to their true proportions, he makes an important contribution toward a necessary general revision of our opinions concerning the *primary* historical rôle of at least the last two factors. Climatic and pathological explanations of historical events have been used very widely and very loosely during the last few decades, only to crumble every time the respective problem has been examined in detail and in all its ramifications.

Titiev tries to give not only a description, but also a deeper understanding of the extremely complicated and varied ceremonialism of the Hopis in abstracting the fundamental ideas underlying the numerous rites, ideas which find expression also in the Hopi calendar. The most important point seems to be that where we see life and death as two opposed categories, the Hopis see only one whole composed of two life cycles, one in the upper, one in the lower world, supplementing each other. This supernatural extension of their life sphere, re-enacted in their rites, supplies the Hopis with the all-important assurance that in spite of a hostile environment, they cannot be destroyed.

ERWIN H. ACKERKNECHT

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NAVAHO WITCHCRAFT. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University. Volume XXII, Number Two.*

By Clyde Kluckhohn. Published by the Museum, Cambridge, Mass. $2.25 (paper). x + 149 pp. 1944.

During the last sixty years a great body of excellent information concerning Navaho food, Navaho techniques (blankets, silver-work), and Navaho religion and its ceremonials (chants, sandpainting) has been collected. Yet almost no attention has been paid to what the Navahos themselves refer to as the "bad side" of their supernatural techniques and beliefs. This is largely explained by the fact that information on witchcraft, the greatest of all crimes, is very difficult to obtain in Navaho as well as in most other primitive cultures. Only an ethnographer extremely familiar with Navaho folkways and the Navahos themselves, such as Kluckhohn, could fill this essential gap in our knowledge and understanding of Navaho culture. The merits of Kluckhohn's monograph are not limited to the rather narrow field of "Navahology." His intelligent discussion of one particular case of witchcraft contributes essentially to a better understanding of the whole phenomenon, which seems to be connected with a certain "paranoid" attitude, one of the basic traits of human mentality, collective and individual. The author himself alludes to such larger implications, calling the Navaho belief in witchcraft a "substitute for race prejudice."

In a descriptive part, Kluckhohn formulates the different forms of witchcraft belief, as he found them among the Navahos. A large part of the raw material from which this part is abstracted is given as an appendix. In an interpretative part, he emphasizes the relatively limited disruptive consequences of witchcraft in this given culture, the increase of witchcraft beliefs in periods of heightened socio-economic tension, and the functional rôle which witchcraft plays in Navaho society. Though at a high cost, the witchcraft belief provides at least certain legitimate ways to display anxiety and aggression. It has a certain controlling effect upon the rich, and the powerful singer, a certain protective value for the destitute. It provides an explanation for a number of startling phenomena. From witchcraft beliefs, certain conclusions can be drawn as to objective and subjective situations in Navaho life, productive of strains and stresses.

E. H. ACKERKNECHT

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THE ABORIGINAL CULTURE OF THE CÁHITA INDIANS. *Ibero-Americana: 19.*

By Ralph L. Beals. University of California Press, Berkeley and Los Angeles. $1.25 (paper). x + 93 pp. 1943.

The Cáhitas are a complex of closely related Indian tribes living near the Mexican border between the states of Sonora and Sinaloa. They are much alike in all phases of their culture except language. This fact was observed by the Jesuit missionaries of the sixteenth century who found that every time they crossed a watershed they were obliged to learn a new idiom.

This fact would seem to indicate that travel was not a luxury in which the Cáhitas indulged. And no wonder! Water, the most indispensible requisite for the support of any kind of life, is notoriously scarce on the shores of the Vermilion Sea. In midsummer there may be cloudbursts in the mountains and then the rivers may rise, traversing their channels with such violence that a crossing is impossible without danger to life and limb; then the waters subside as quickly as they rose, and the stream bed again becomes a desiccated arroyo from which water may be obtained only by digging. The Indian dares not travel far from the water which not only supports his own life, but upon which he has learned to depend for irrigation of his crops as well.

The author of this work learned by experience that each tribe of Indians was acquainted with the contiguous tribes, but could tell him nothing about those living at more remote distances, another fact which testifies of the extent to which the Indians are fettered to the soil.

This work is not indexed, but its table of contents is detailed, and the material is so systematically organized that the lack of an index is not a serious defect. Every phase of the cultural life of the Indians is abundantly covered. First the elemental needs of food, clothing, and shelter are discussed; then the social, industrial, and political details of their life, with such other subjects as their use of tobacco, their recreations, and their religious ceremonies are taken up in order. The work is well illustrated by both plates and text figures, and there are tables setting out certain meteorological data.

The only adverse criticism that the reviewer might make of this study is the omission of any mention of the two most interesting tribes from this area. Probably neither one is Cáhita. The first of them is the Seri tribe, whose native habitat is on Tiburon Island, but who have recently migrated to the mainland to take advantage of the pecuniary opportunity afforded by the fishing industry. When the Spaniards discovered the Gulf of California, the Seris were living in a neolithic culture, and as late as the end of the nineteenth century they occasionally indulged in "long pig."

The other tribe is that of the mysterious blond Indians from the valley of the Yaqui River. Rumors of blond Indians are nothing new; they are at least as old as the time of Balboa and occur everywhere from the Orinoco to Baffin Bay, but the report of blond Yaquis seems to rest on better evidence than most of them. President Alvaro Obregon had red hair, a fact which accounted for the now discredited belief that the original form of his patronymic was "O'Brian"; and Cajeme, the chieftain who successfully defied Porfirio Diaz, and who is claimed by both the Yaquis and the Mayos, is said to have had yellow hair and blue eyes. Cajeme has not been dead long enough to have become a tradition—he is remembered by people now living—and it ought not to be difficult to check up on his complexion. It is important that this be done before it is too late, as a recent author reports a Seri tradition of a mysterious ship, manned by tall blue-eyed sailors who spent a winter at Kino Bay harpooning whales and boiling their blubber in caldrons long before the visit of Francisco Ulloa to these shores. From this the author concludes that the blood of the Norsemen flowed in the veins of Cajeme, and that his blond complexion was a heritage from this ancestry. Speculations of this nature may appeal to one's sense of the romantic but should not be accepted unless based on convincing evidence, and it is unfortunate that the author did not include the blond Indians in his survey so that he might have either confirmed or denied their existence authoritatively.

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SOME EARLY SITES IN THE NORTHERN LAKE TITICACA BASIN. *Peabody Museum of American Archaeology and Ethnology, Harvard University. Volume XXVII, Number One.*
By Alfred Kidder, II. Published by the Museum, Cambridge, Mass. $1.25 (paper). vii + 48 pp.; 7 plates. 1943.
ARCHEOLOGICAL REGIONS OF COLOMBIA: A CERAMIC SURVEY. *By Wendell C. Bennett.*
EXCAVATIONS IN THE VICINITY OF CALI, COLOMBIA. *By James A. Ford.*
Yale University Publications in Anthropology, Numbers Thirty and Thirty-One. Yale University Press, New Haven; Oxford University Press, London. $2.50 (paper). No. 30, 120 pp.; 12 plates. No. 31, 79 pp.; 4 plates. 1944.
PERUVIAN ARCHAEOLOGY IN 1942. *Viking Fund Publications in Anthropology Number Four.*
By A. L. Kroeber. The Viking Fund, Inc., New York. $3.00 (paper). 152 pp.; 48 plates. 1944.

Between the archeology of the New World and that of the Old there is a great gulf fixed. Upwards of three millennia ago the Phoenicians had perfected a system of phonetic writing, while the inhabitants of the plateaus of Anahuac and Tiahuanaco, despite the relatively high degree of civilization which they had achieved at the time of the conquest, still had to have recourse to a system of hieroglyphics comparable to that of the early dynastic periods of Egypt. Our knowledge of the early civilizations of the Mediterranean basin comes largely through the Rosettta Stone, upon which is incised the same text in hieroglyphic, hieratic, and phonetic scripts; but there can be no Rosetta Stone to help us unravel the megalithic inscriptions of Yucatan or the mnemonic quipus of Cuzco and the Titicaca region.

In the Old World, history and archeology have joined hands, and in what they reveal to us of the glory that was Greece and the grandeur that was Rome we can recognize the handiwork of our own intellectual ancestors in the Parthenon and the Coliseum. But the builders of the pyramid of Tenayuca and the serpent mound in southern Ohio are forever surrounded by a screen of impenetrable mystery, and we can know no more of them than did Shelley of Ozymandias. For this reason even the most scholarly reports of American archeological investigations contain little to stir the imagination. There is nothing among them comparable to Schliemann's discovery of the site of Troy, or Carter's excavation of the tomb of Tut-ankh-amen. Even the gold artifacts of Monte Alban, sensational as they were when first announced, have been largely forgotten today because they could not be connected to anything that seems familiar to us.

The three works under discussion here consist largely of inventories of potsherds, with annotations as to whether or not they were colored or glazed, whether or not they had handles, what purposes they might have served, etc. Such data, while undoubtedly of importance to the specialist, are likely to have but little interest to the more catholic devotee of archeology. They are significant partly because potsherds are frequently the only remaining evidences of vanished cultures, and partly because they may reflect differences among separate cultures.

But those who wish more dramatic evidence of vanished peoples may find them in the architectural remains uncovered in the Andean highlands. In the Titicaca basin the Peabody Museum has excavated a temple of astonishing size, the foundation of which consists of rectangular blocks of stone approximately 8 x 3 x 2 feet in size. It is the most complex edifice yet discovered in the region, though it may be surpassed in future investigations.

At San Augustín, in western Colombia, a Yale University expedition has uncovered a quantity of carved rocks. Some of these appear to be boulders, and mark the site of tombs, but others are part of the bedrock and are still *in situ*. Some of these carvings represent animals, and others are geometrical designs. The people who carved them were also expert goldsmiths, if one is to judge by the illustrations of gold artifacts from the same locality, now in the museum at Medellín.

But to the reviewer the most interesting feature of any of these expeditions is the wooden "Stonehenge" at La Estaquería in southern Peru. This structure, which has never been illustrated before, so far as the author is aware, consists of a multitude of trunks of algarroba trees set up vertically over an area of approximately 800 square meters. Algarroba wood is extremely tough and durable, and has been used for lintels in stone walls of undoubted pre-Hispanic origin, for which reason the author suggests that these wooden steles would afford an excellent opportunity for a tree-ring study. This is especially true because living algarroba trees are readily available nearby for comparison.

All three reports are extremely well prepared, and the plates, some of which are photographs and some drawings, are among the best that this reviewer has ever seen. The reports are thoroughly indexed, and excellent examples of what such reports ought to be. That dealing with Colombia has an introduction, dealing with the geography of the area, which makes intensely interesting reading.

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THE AMERICAN CHARACTER.

By Margaret Mead. Penguin Books (Pelican Books), Harmondsworth and New York. 9d (paper). 173 pp. 1944.

Two-thirds of this book is devoted to an analysis of the American character, the author taking her clues from the way young Americans are raised. Her result is the following:

> "We have a certain kind of character, the American character, which has developed in the New World and taken a shape all its own; a character that is geared to success and to movement, invigorated by obstacles and difficulties, but plunged into guilt and despair by catastrophic failure or a wholesale alteration in the upward and onward pace; a character in which aggressiveness is uncertain and undefined, to which readiness to fight anyone who starts a fight and unreadiness to engage in violence have both been held up as virtues; a character which measures its successes and failures only against near contemporaries and engages in various quantitative devices for reducing every contemporary to its own stature; a character which sees success as the reward of virtue and failure as the stigma for not being good enough; a character which is uninterested in the past, except when ancestry can be used to make points against other people in the success game; a character oriented towards an unknown future, ambivalent towards other cultures, which are regarded with a sense of inferiority as more coherent than our own and with a sense of superiority because newcomers in America display the strongest mark of other cultural membership in the form of foreignness."

The author analyses the American character for a specific purpose: to find out in which way the maximum energies of this given character can be mobilized for winning the war. In the last third of her book, Mead develops the goal that in her mind would release this maximum energy: a new synthetic world culture, engineered by Americans on the basis of the "peculiar blend of moral purpose and practical inventiveness" that makes up the American character.

Though Mead's highly interesting book (which was published in this country two years ago under the title *And Keep Your Powder Dry*) deserves detailed discussion, this journal seems not to be the place for it. Though probably not inferior in quality to the author's former publications, which have made her one of the leading anthropologists of our time, this highly emotional book is definitely of a different quality, as it is built on premises and pursues goals which are not those of scientific treatises.

ERWIN H. ACKERKNECHT

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FOOD ENOUGH. *Science for War and Peace Series.*

By John D. Black. The Jaques Cattell Press, Lancaster, Pa. $2.50. vii + 269 pp. 1943.

Black, professor of economics at Harvard University, in this book sets forth clear, pointed arguments relating to the necessity for the production and effective distribution of "every possible pound of human food" at the present time. The food needs of the armed forces, of war workers and other civilians, of our allies, via Lend-lease and UNRRA, are plotted on the basis of realistic postulates and the most recent statistics. Germany's food picture is also surveyed and found to be not too great a weakness in her military situation. Consideration of problems of production resulting from the manpower situation, from the lack of farm machinery, from the needs for non-food crops, and from the relation between what we need, what we could produce, and what we can afford all lead up to the question of desirable shifts in production and consumption. The program Black outlines calls for less meat and more milk, eggs, peas, beans, peanuts, and soybeans; less animal fat and more vegetable oils; more potatoes; and tomatoes, carrots, and other vegetables and fruits that can be produced with relatively little labor instead of those that require a lot. In discussing food prices and rationing and the general problem of distribution, Black pulls no punches in criticizing past and present policies and practices. He ends by summarizing the program of the United Nations Food Conference of 1943 to achieve world-wide freedom from hunger, and by discussing the necessary elements of international cooperation in this field.

This is an excellent treatment of the interrelations of nutrition, agriculture, economics, and human relations in the current situation, written for the layman in non-technical style. The only obvious criticism—one beyond the author's control—is that events have moved so rapidly and conditions have altered so markedly since August, 1943, that much of the program will already need modification. The main points, however, will not have altered. In-plant feeding will still be desirable for war workers; soybeans will still be needed as never before; civilians should still make shift with less meat; and more thought and careful planning will be required before the world's hunger is stilled.

BENTLEY GLASS

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ON LIVING IN A REVOLUTION.

By Julian Huxley. Harper and Brothers, New York and London. $2.50. xiv + 242 pp. 1944.

This collection of essays is assembled, with a few new offerings, from magazine articles published during the war years. Certain of them bear directly on Huxley's views of the world situation today. Briefly: we are experiencing, in the war, one symptom of a world revolution. The inevitable trends of this revolution are, within nations, toward the subordination of economic to non-economic motives, toward more planning and a more conscious social purpose; internationally, toward greater organization and a fuller utilization of the resources of backward countries. The revolution may assume either a democratic or a totalitarian form, the latter being self-defeating in the end. The only universal mark of democracy is the satisfaction of the needs of individuals, their welfare, development, and active participation in social processes, and eventually their equal cooperation in international organization. The revolution, like the war, must involve our conscious acceptance and participation, in either a democratic or a totalitarian way. These ideas are set forth in the first essay, reasserted in the second, and reiterated in the third, with echoes and reverberations in the majority of the remainder. Notwithstanding general agreement with Huxley's point of view, one could wish that repetition had not been carried to the point of diminishing returns. However, in some of the essays, such as "Colonies in a Changing World" and "Reconstruction and Peace," these views are applied to the solution of postwar problems; and definitely new ground is broken in "Education as a Social Function," in which Huxley calls for the application of scientific treatment to education and suggests the need for adapting it to social trends.

Biologists will find most pertinent the essays on "War as a Biological Phenomenon" and "Darwinism Today." These are excellent summaries of subjects developed at greater length in *Evolution: the Modern Synthesis*. "Philosophy in a World at War" represents Huxley's matured monistic philosophy, which places man at the end of the line of evolutionary progress, one who "stands alone as the agent of his fate and the trustee of progress for life." These ideas, also, Huxley has amplified in the magnum opus referred to above and in *Man Stands Alone*. The essay on "'Race' in Europe" is a digest of *We Europeans*. "Birds and Men on St. Kilda" and "Animal Pests in Wartime" are very interesting studies of man's relations to animal populations.

Altogether, while one familiar with Huxley's work will find here little that is wholly new, there is vigor and a modicum of fresh thought that is stimulating, and as a summary of Huxley's thinking the collection is valuable. And everyone, I am sure, will enjoy Dr. Spooner, who somehow, in his characteristic way, wandered irrelevantly into this book.

Bentley Glass

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

Science and Criticism: *The Humanistic Tradition in Contemporary Thought.*

By Herbert J. Muller. Yale University Press, New Haven. $3.75. xiv + 303 pp. 1943.

A more or less satisfactory compendium of achievements in one or more of the sciences is easily found. The desire on the part of some scientists to have their work more widely understood, and the desire of many laymen to find some reassurance through comprehending the very real achievements of science, take care of this.

Herbert J. Muller has also set out to further the general understanding of modern science, but his book has more than usual value because it is written with a rather specific purpose.

In the first place, he considers not the concrete achievements, but the current theoretical concepts of physics, biology, psychology, and the social sciences. These concepts, conflicting and controversial as they are, often providing fields for acrimonious debate and undebatable prejudice, he has reviewed with a rare combination of critical judgment and sympathy.

The second distinguishing feature of *Science and Criticism* is that it was written for the critic. It is designed to show him how the theories and attitudes of modern science can contribute to his work of criticism. This aim leads to a statement of the outlook of scientific humanism, its relevance to the present day situation, and its value for the critic.

One does not have to enquire into the author's qualifications as an interpreter of science. His treatment of the material is evidence enough of his ability to seek and evaluate without arbitrary judgment, whether in applause or condemnation.

Science and Criticism is intended primarily for the literary critic; but inasmuch as we are all critics, of life if not of literature, it will have a very general interest and use.

Eileen Sutton Gersh

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A Shorter History of Science.

By Sir William Cecil Dampier (formerly Whethem). Cambridge: at the University Press; The Macmillan Company, New York. $2.00. x + 189 pp. 1944.

This meaty little volume is a masterly condensation of the author's *History of Science*. It is designed for the benefit of "older schoolboys" and the "general reader." The sections dealing with the philosophical and religious implications of science have been drastically cut, although the reader is always made aware that science is no mere bag of technological tricks. Following the tradition of his great predecessor, Whewell, at Trinity College, Cambridge, Dampier has given the physical sciences a central place, which is as it should be in a general history. This story of the development of the physical sciences is told with a force, comprehensiveness, and insight that are unmatched in the English language. The focus is held steadily on the great themes—stars and atoms, matter and force—but the mass of lesser topics is prodigious, skillfully organized, and ranges all the way from dynamos to Robinson Crusoe.

Undoubtedly the weakest part of the book is that concerned with the biological sciences. The eugenical and sociological views that crop out in several places can only be called a minor scandal. It may be that Rome fell because the purity of its blood had been corrupted by foreign elements. It may be that the old landed families of England have more genes for great scientific ability than any other group in the population. We would only ask, in the broken English of a distinguished American physiologist, "Vot iss de effidence?" The explanation of such statements seems to be simply that the author has been so caught up with the rush of discovery in the physical sciences that he has not had the time to reinvestigate such questions since his own work in 1909. The eugenics is scarcely Galtonian. It seems incredible today that no distinction should be made between chromosomal and cultural inheritance. The anthropology is mostly Frazer's *Golden Bough*. Malinowski is not even mentioned in the index.

Several common errors have crept in. Schleiden and Schwann are credited with the cell theory and specifically with having traced the cells back to their origins in the embryo. The relative space given to various biological topics and individual investigators is sometimes surprising. Pasteur's biological work fills three lines. Lady Mary Wortley Montagu receives slightly more.

It has been suggested that this little book is perhaps too condensed for the general reader or for school use. However, in any book that is to be kept down to a reasonable size, the actual choice is not between a condensed mention and a full explanation but between a mention and nothing. We are convinced that far better results are achieved both in stimulating interest and in imparting the truth by at least telling the boys, as Dampier does, that after some two thousand years Lobatchevsky has succeeded in seeing through Euclid, and Cantor in resolving the paradoxes of Zeno, then by silently implying that Euclid and Zeno have said the last word. Of course, the only scientific way to determine how useful this book will be for the older schoolboy is to try it on him in statistically significant numbers and find out.

G. B. MOMENT

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MEN OF SCIENCE IN AMERICA. *The Role of Science in the Growth of Our Country.*
By Bernard Jaffe. Simon and Schuster, New York. $3.75. xl + 600 pp. 1944.

Slightly over ten years ago I found Jaffe's book *Crucibles* intensely interesting, helping to make real to me some of those chemists previously only names in books. I therefore picked up his widely heralded new book on American science and scientists with keen anticipation. It must be set down, however, as disappointing in some respects although excellent in others.

The general plan, that of weaving the entire history of American science around certain outstanding figures in a variety of fields, is well conceived. The effort to show the influence of their times on these men, and their reactions to political, social, and economic problems is consistent, if at times, perhaps, rather overstrained. The choice of central figures is very good, and equally representative of the physical and biological sciences, only psychology having been ignored. The list begins with Thomas Harriot, early naturalist and mathematician, and passes chronologically to Franklin, Benjamin Thompson, Thomas Cooper, Rafinesque, Say, Morton, Henry, Maury, Agassiz, Dana, Marsh, and Gibbs in the nineteenth, and Langley, Michelson, T. H. Morgan, Herbert M. Evans, E. P. Hubble, and E. O. Lawrence in the present century, making eleven men in the physical sciences and eight in the biological. This is preeminently a list of workers in "pure" science, not in invention or applied science. No two writers, perhaps, would pick out exactly the same group of scientists, and Jaffe's choice is certainly thoughtful and well balanced. The accounts are vivid and abound in anecdote and interesting detail. The plates supply good portraits of the central figures.

On the other hand, Jaffe's style has not improved with the years. There are too many pronouns of dubious antecedents; too many misused words; too many unhappy expressions. The organization of material within the individual chapters does not appear to have been so carefully planned as the larger organization of the book; the chronological pattern tends to become obscured by abrupt transitions back and forth.

In the chapter on Thomas Hunt Morgan and the rise of American genetics more serious defects are to be found. It is amply evident that, however lucid and accurate his discussions of physical science may be, Jaffe is not at home in the intricacies of genetic principles. There are many minor slips that may be apparent only to geneticists and do not affect the thread of the story. However, when Jaffe comes to relate how Mrs. Morgan discovered the flies with attached-X chromosomes, he becomes utterly confused. The attached-X females are metamorphosed into gynandromorphs (one is even illustrated), and Mrs. Morgan is said to have "bred thousands of this queer intersex race of flies, crossbred them, interbred them," and more similar nonsense. A little farther on, Muller is said to have "actually transmuted species and created new ones by exposing flies to the action of ordinary X-rays!"—a remark that will certainly cause him distress. The whole fabric of confidence in a writer's carefulness and accuracy is so undermined by this tissue of errors that one would be tempted to condemn the entire book, were it not that in the next chapter Jaffe does a creditable piece of reporting on the research upon hormones and vitamins. A biologist may assume that the accuracy of the other sections is probably fairly high and excuse Jaffe on the ground that he is not the first to err egregiously when trying to write about genetics.

This is a stimulating book in spite of its glaring defects. It presents a comprehensive view of the growth of American science that fills a real gap in our accounts of the development of science.

BENTLEY GLASS

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SCIENCE IN THE UNIVERSITY.

By Members of the Faculties of the University of California. University of California Press, Berkeley and Los Angeles. $3.75. x + 332 pp. 1944.

It is an unexpected pleasure, in these days of cheaply produced wartime books printed on inferior paper, to pick up a really excellent example of book-making such as this volume celebrating the Seventy-fifth Anniversary of the founding of the University of California. One can only wonder how the publishers managed to do it.

The contents include nineteen essays by members of the faculty, each presenting a picture of a limited part of the scientific research that has made the University of California, from its earliest days, a leader in this respect. The articles are varied not only in content but also in style and purpose, having in common chiefly their aim to create unitedly a panorama of interesting research that will inform fellow scientists and educated laymen of the achievements of research in the institution. Some few articles are so technical that they will be appreciated only by specialists in the author's field. Others are written in simple and non-technical language for every citizen to read. The majority fall in between.

Robert Grant Aitken summarizes first the general development of astronomy from the time of Galileo. J. R. Oppenheimer covers the progress of the study of cosmic radiation since 1936. The discussion of molecular forces and solubility, by J. H. Hildebrand, is exceptionally illuminating, and biologists will find it well worth their while to read it. The contribution of Carl L. A. Schmidt on the chemistry of the amino acids and proteins is only too brief. A survey of the history of organic chemistry, by G. Ross Robertson, emphasizes rather more than do the previous essays the contributions of Californian science.

Jakob Bjerknes provides a clear account of the factors involved in the rise and fall of barometric pressure, and H. U. Sverdrup of the Scripps Institute of Oceanography writes on the California current, a subject that will especially interest ecologists. Wm. C. Putnam's account of the geological evolution of the Mono Basin during the Pleistocene is very interesting. One wonders why, in so richly illustrated a book, he did not include at least a few photographs of this Sierran landscape. U. S. Grant IV discusses the more technical topic of the causes and amounts of subsidence and elevation in the Los Angeles area in recent years, some of the subsidence being man-made.

The biological contributions begin with a very general essay by O. L. Sponsler on modern conceptions of protoplasm Richard Goldschmidt follows this with a review of the evidence that has led him to regard genetic changes as resulting from rearrangements of chromosome material and to dispense with the older idea of gene units. Geneticists will find this controversial matter interesting, but to others it will no doubt seem the most technical article in the volume. The late C. B. Lipman has vividly described his long-continued experiments on the survival of bacterial spores in centuries-old mud bricks from California and Peru. Claude ZoBell, of the Scripps Institute, writes on the relation of the study of the sea to man. Ralph Chaney, in a beautifully illustrated article, considers the paleobotany of California; and L. Miller, the recent evolution of California's birds. D. R. Hoagland's treatment of general aspects of the study of plant nutrition is excellent. J. M. D. Olmsted writes on the place of physiology as an independent science, Knight Dunlap on the contributions of psychology, and S. J. Holmes concludes the volume with an essay on evolutionary ethics. The latter is a penetrating criticism of Thomas Henry Huxley's Romanes lecture of 1893, and comes to much the same conclusions about the origin of ethical values as those recently published by Julian Huxley. The contribution by Dunlap is marred by dogmatic statements and a general tendency to attribute his own views to all psychologists. Geneticists will be astonished at the view he expresses that about hereditary traits nothing can be done, and that heredity is not among the real (sic!) causes of traits. Nevertheless the article is stimulating and presents a valuable survey of recent trends in psychology.

All in all, the University of California has ample reason to congratulate itself in being so well presented to both scientific and lay publics in this volume.

BENTLEY GLASS

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ALASKA DIARY 1926–1941.

By Ales Hrdlicka. The Jacques Cattell Press, Lancaster, Pa. $5.00. xv + 414 pp. 1943.

During his trips of exploration it was the custom of the author to record, aside from his scientific work, daily notes of current events and experiences. It is these notes of his 1926–1941 expeditions to Alaska which have been gathered together in the present volume.

They are, as Doctor Hrdlicka states in his preface, "just brief but faithful records of what befell or was encountered by the writer and his coworkers in those far-away and lonesome, yet scientifically important regions, in quest of anthropological information." As is to be expected, such notes contain numerous items that are more or less relevant and complementary to the scientific results proper which have been published elsewhere.

Throughout the records, considerable attention has been given to the weather, to food, and to transportation, for, as the author points out, these factors are constantly with one in the Far Northwest and not seldom prove of paramount importance. They can thwart or make very difficult the best laid plans or again facilitate them. "Mind, health and physical strength, however necessary, are alone often powerless in these parts. Man is here against the elements, against want of things and means, and must repeatedly give way." Often the brief sentences (almost telegraphic in style) reflect the suffering from the hardships of the days—the cold rains, the storms, the weariness of effort, the lack of facilities, the pests of mosquitoes and gnats. But there is also a brighter side. As to illness, we are told that "there is something strange and most grateful in this respect in Alaska." Apparently there is an actual absence of many of the common viruses and bacteria. Wholesome hunger never fails and all digestive troubles vanish. "What would many a city dweller give for the Alaska hunger—with the dreamless refreshing nights; and the rest of us for the pure cool Alaska water." The water, we are told, is mostly so good that one grows almost addicted to it! The mountain scenery is superb, and for the anthropologist there is always the constant tonic of new discoveries.

The ten seasons, in all, spent in Alaska by the author have thrown substantial new lights on the problems of the peopling of America. Where before there was but a haze of opinion, there are now definite facts substantiated by large collections. Nearly 4,000 crania and skeletons have been collected or excavated and have afforded a solid basis for important conclusions. The present text shows how many of these collections were made and what, in general, they embrace. So far, what the work has made possible, we are told, is the recognition of the archeological riches of the region; of the direct connection of these remains and their people with Asia; of the presence of hitherto unsuspected old human strains in the territory; of the high material cultural status of the occupants of the region in prehistoric times; and of its connections anthropological as well as archeological, with the rest of continental America. While much has been accomplished there is yet much to be done. According to the author, there is enough left in Alaska to occupy American anthropologists and archeologists for generations to come, and to give a wealth of additional materials.

The text is abundantly illustrated with some 200 photographs which in themselves are extremely interesting. The volume is also well indexed.

MEET MR. GRIZZLY. *A Saga on the Passing of the Grizzly.*

By Montague Stevens. The University of New Mexico Press, Albuquerque. $3.50. x + 281 pp. 1943.

This is a book for sportsmen who will be delighted with these highly entertaining, rambling memoirs of the author, an old English gentleman who became a rancher in western New Mexico some sixty years ago. The accounts of hunting and of training dogs and horses contain much that is original and informative, and the thrilling advantures with animals and men are well worth reading. The author assembled and trained with exceptional care effective packs of dogs for trailing and fighting bears, and succeeded in killing numerous black and grizzly bears.

The naturalist and the psychologist can find among these reminiscences unusual and detailed observations on animal behavior, although, in spite of the title, there is much more pertaining to dogs, horses, and men than to bears. Of greatest interest are the lengthy descriptions of the remarkable accomplishments of bloodhounds in trailing man and beast, and of the author's success in making his hounds comprehend what is expected of them. The nature of the grizzly bear is not as fully depicted in the present volume as it has been in various other publications, particularly in that great old book by W. H. Wright, *The Grizzly Bear* (New York, 1909).

EMULSION TECHNOLOGY, *Theoretical and Applied, Including the Symposium on Technical Aspects of Emulsions.*

Edited by H. Bennett. Chemical Publishing Company, Brooklyn. $5.00. xi + 290 pp. 1943.

This book contains the twelve papers originally published by the same publishers in 1935 under the title *Technical Aspects of Emulsions.* This was a collection of papers read at a symposium held in London on December 7, 1934, by the British Section of the International Society of Leather Trades' Chemists. The present volume contains these original papers, almost unchanged except by the addition of many unnecessary commas, and three new articles. This new material, not clearly indicated as such, consists of the papers by Cobb, by Hofmann, and by Werthan, and an index. The material written in 1934 has not been brought up to date in subject matter or bibliographies, although there have been developments in these fields since that time.

Certain sections of this book may have interest and value for those working in biological fields. The first paper, "On the Mechanism of Emulsification" by Herbert Freundlich, deals with the production of emulsions by ultrasonic vibrations, and may interest those concerned with the physiological aspects of ultrasonics. The brief paper by Walsh and Frazer on "The Use of Highly Dispersed Emulsions in the Treatment of Toxaemic Conditions" should be of interest to readers of this journal, although it must be borne in mind that this paper was written in 1934. Two other papers deal with subjects related to the biological field, that by Corran on "Some Observations on a Typical Food Emulsion," namely mayonnaise and salad dressing, and that by Woodman on "Problems Connected with the Preparation and Application of Emulsions Used in Agricultural Spraying." The latter paper is long (43 pages); the author discusses various types of emulsions, their preparation, stability, and effect upon various insects and plants, and includes a 5 page bibliography.

Those interested in the preparation of emulsions will find the new article by Cobb on "The Fundamental Principles of Practical Emulsion Manufacture" to be specific and practical indeed. It should prove useful to any who may wish to make, alter, or keep an emulsion. The new paper by Hofmann on "Industrial Emulsion Formulation" is also specific and includes formulas for household and pharmaceutical products. The paper by R. I. Johnson on "The Design of Emulsifying Machines" contains descriptions of industrial emulsifiers of various types, all of large capacity, though mention is made of laboratory and hand type homogenizers.

The remaining articles deal with such subjects as paints, leather, and asphalt, and would appear to have little direct relation to the field of biology.

Belle Otto

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THE QUARTERLY REVIEW of BIOLOGY

PHYSIOLOGICAL COMPETITION AS A REGULATORY MECHANISM IN MORPHOGENESIS

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INTRODUCTION

THE major purpose of the present paper is to formulate a theory for a regulative principle of developmental processes. In the course of the analysis it is further proposed to examine in some detail the consequences of the principle of physiological dominance and the gradient theory from which it arose. It will be indicated that the deduction of regulation from the gradient concept requires auxiliary assumptions concerning the mechanisms through which gradients affect the course of development. A mechanism first used by Barth (1938) will be generalized and rigorously developed. The development will permit an examination of its adequacy as a regulatory mechanism. The biological field theory will also be considered, with a view to extending the principles of competitive interaction to a field concept. A method for an extension of this kind will be briefly discussed. Finally, it is important to note that the quantitative data on coelenterate regeneration has served as the main guide for the present analysis, although a broader basis is adopted in the discussion wherever possible.

THE PROBLEM: LIMITED REALIZATION

The fact that many pathways leading to different end results exist, and yet the processes of normal development and regeneration follow a particular one is one way of posing the fundamental problem of embryology. Attempts at the solution of this problem become a search for a regulative principle.

It is known, for example, that if the early blastomeres of some eggs are separated, each is capable of giving rise to a complete and perfectly proportioned embryo. Yet in the normal course of events this potentiality is not realized, each blastomere giving rise to but a part of an embryo. The central problem here is to find the regulative mechanism which successfully limits these capabilities.

Numerous experiments have indicated that for organs and organ systems the field capable of differentiating into a particular structure is more extensive than the area which actually forms the organ under normal conditions. Here again a limitation of potentialities is obtained, in that only a fraction of the field potency is realized. Hydranth reconstitution in the coelenterates, entailing as it does the suppression of all but apical hydranths, presents a particularly well-examined instance of such regulation. Though little direct experimental confirmation exists for it, the gradient concept first proposed by Boveri in 1901 and brought to its full development by Child (1941) has of late received wide acceptance. In more or less direct support of the gradient hypothesis, we may cite Adelmann's (1929a, b) work on eye development as well as a detailed study of gradients in coelenterates and planarians by Child and his coworkers, to which we shall return. However, it has been the many verifications of its indirect consequences that has been the stimulus for the wide adoption of the gradient viewpoint. But its use in the interpretation of developmental phenomena has not been entirely uncritical. Gradients have been used by not a few authors to explain the partial realization of potencies without any supplementary arguments as to how the latter is effected. Thus, to say that the realization of field potencies in actual development is *localized in the high region of the potency gradient* is little more than a restatement of the observation. It must be emphasized that the existence of two regions with different capabilities for differentiation does not of itself imply the necessary suppression of the one with the lower power to transform. The explanations in terms of gradients alone tacitly make use of this implication, and in so doing lose sight of the crux of the problem, namely, the mechanism involved in the suppression of existent potentialities.

From the available information two concepts emerge which are basically important for the present analysis. The first is the postulated existence of gradients in differentiation power along one or more axes of a morphogenetic field. The second is that as a result of some as yet unknown regulative mechanism, a principle of potency limitation is apparently followed during normal development of organismic pattern. This principle may well be called the *principle of limited realization.*" These two concepts cannot be regarded as isolated or unconnected. Clearly, if one of two regions is to succeed in the completion of a process of which both are capable, it is not conceivable that they both have equal ability to do so. The very fact that one goes to completion and the other does not would indicate that a difference must exist, and if this difference varies in a reasonably continuous fashion, it may well be called a gradient. In other words, the facts would appear to demand that a necessary condition for the suppression of the inhibited group is that some kind of a gradient should exist between it and the successful one. Nevertheless, while a gradient is necessary for a suppression of this nature, it is not sufficient in itself to bring it about. The necessary condition, however, makes the gradient concept a logically indispensable part of any theory which seeks to explain the principle of limitation. This then leaves open the question of what other postulate can be selected which, when used in conjunction with the gradient hypothesis, will make the combination necessary and sufficient conditions for the deduction of regulatory behavior. The central problem may thus be reduced to one of finding a mechanism whereby gradients can be implemented as effective regulatory agents in morphogenesis.

METHODS

Since differentiation is a process taking place in time as well as space, a kinetic analysis will make up a major portion of the present examination. It is important at this point to note the nature of the quantitative data available. When it is desirable to acquire quantitative information on rate or extent of development, it has been customary to select some well-defined stage and measure the time required to reach it. Thus for example, in the regeneration of hydranths in *Tubularia*, the time from cutting to the appearance of a constriction between the hydranth primordium and the rest of the stem has frequently served this purpose. The problem of the interpretation of rates determined in this manner with particular reference to open and closed systems is discussed by Spiegelman and Moog, 1944. In other instances, the actual emergence of the hydranth from the stem has been chosen as the end point of the process. In any case, whatever stage is selected, even though it be the first visible signs of differentiation, it is obvious that a certain amount of differentiation must have preceded it. It is even more obvious that a certain critically minimal amount of differentiation must occur if the organism is to reach some arbitrarily chosen stage.

With this type of data, then, the existence of dominance or the suppression of one of two groups implies only that one of them is capable of reaching a particular stage in development and the other cannot. It does not imply the complete inhibition of differentiation in the dominated group. For this reason a kinetic theory of dominance which seeks to describe the phenomenon in terms of the available data can only do so in terms of the relative amounts of differentiation attained in the interacting groups. That is to say, dominance will be exhibited if it can be shown that as a result of the postulated interaction the dominated group cannot reach either the differentiation level attained by the successful group, nor the level attainable when it is isolated from the dominating one.

The present analysis will not inquire into the origin of regional differences. On the contrary, their existence will constitute the primary assumption of the theory to be developed for potency limitation. Two important questions for which specific answers will be sought are:

1. Admitting the existence of activity gradients, what are the consequences for the development of organismic patterns?
2. What mechanism of a simple nature can be postulated that will provide a reasonable and justifiable explanation for the principle of limitation as manifested by such phenomena as dominance?

The answers to these questions will be obtained for the most part in purely biological terms, a restriction imposed by the almost complete ignorance of the biochemical basis of morphogenesis. It is logically not necessary to make detailed assumptions concerning the nature of the "activity" whose gradient is being postulated. We may with Child call it a gradient of "physiological activity," if nothing further is implied than that gradients in ability to differentiate have been presumed and that these must have a physiological basis. A more precise definition and interpretation will be possible within the formulation of the theory.

THE CONCEPT OF PHYSIOLOGICAL COMPETITION IN DIFFERENTIATION

The interaction theory to be developed in the subsequent sections is based on the following assumptions:

1. All physiologically active biological organisms are open systems (see Reiner and Spiegelman, 1944, for a discussion of the energetics of open systems) through which matter is continually flowing and within which energy is continually being expended to maintain the status quo. (Assumptions 2 and 3 are not strictly independent of 1. The argument necessary to deduce them however would lead us too far from the purposes of the present discussion.)
2. Open systems interact, i.e., influence each other's (physiological) state and activity.
3. Closed systems do not interact in the above sense

To further specify the nature of the biological interaction with which we shall be concerned, we state the following definition of *physiological competition*: Every group of biological units (species, individuals, cells) are in *physiological competition* if,

a. They require and draw upon a common source of food (substrate) and (or)
b. excrete harmful metabolites into a common environment.

Both of the biological interactions mentioned in the above definition are competitive, the first obviously so, while the second may be reduced to a competition for what can be called "biological or physiological space." Every cell (or organism) requires for its continued existence not only the space it occupies physically but also enough of its environment to dilute its waste products below a critically harmful level. It is in this sense that we may speak of competition for space as well as food.

In order to apply the above assumptions and definition to the particular problem of cellular differentiation it is necessary to postulate the following:

4. The transformation of a group of indifferent cells into a more highly specialized tissue requires the synthesis of new structure, and this synthesis involves the expenditure of energy.
5. A mechanism must exist involving the breakdown of some energy-rich substrate to supply the necessary energy.

In these terms, two groups of cells transforming into the same structure and coexisting in the same physiological environment will compete for the energy-rich substrate.

It is the task of the succeeding sections to deduce the consequences of this kind of competition for the transformation, and its kinetics. One of these consequences, because of its importance, may be mentioned here. It follows from assumption 1 that when a structure is complete and no additional material is being synthesized, a steady and minimum supply of the energy-yielding substrate is still necessary to keep the system intact. This dynamic view of structural stability receives strong experimental support from the work of Schoenheimer and his coworkers (1940a). As will be seen, this has important implications for the process of differentiation, for it implies that a fully differentiated structural unit does not, by its completeness, remove itself from the common physiological space.

TRANSFORMATION WITHOUT INTERACTION

Consider a group of cells in a 'neutral' environment and physiologically isolated from any other group going through the same process. Absolute neutrality of the environment as well as complete isolation are of course impossible of attainment, but experimentally, the ideal may be roughly approximated. For the purposes of comparison it is sufficient that some particular set of experimental conditions be selected as standard, and all other data may be compared with the results obtained from it. Let the mass of cells be M. At the beginning of the observations they are all type-n having a mass N. Type-n cells differentiate into type-r, having a mass R at any t. With progressive differentiation N decreases and R increases. We shall for the moment assume that during the period of observation, ordinary growth in mass or numbers does not accompany the differentiation to any significant extent. This assumption, while not entirely necessary, is helpful if the examination is to be focused on the transformation processes.

Since the mass of tissue, M, remains constant, we may write that, throughout the period of observation,

$$M = N + R \tag{1}$$

If the time course of the process is to be studied, a basic assumption governing the kinetics must be made. Let us assume that the rate at which the n-type transforms into the r-type is proportional to N, the mass of the n-type present at any given moment. That this is a reasonable assumption is apparent from the fact that if it is desired to measure rate of differentiation in terms of *mass of tissue transformed per unit of time*, then it would seem that the greater the amount of the original type present, the larger will the measured rate be. This assumption of proportionality leads to the equation

$$\frac{dR}{dt} = bN \tag{2}$$

The b in equation (2) is a constant of proportionality with an important biological interpretation. It will be noted that it represents the ability in terms of mass per unit of time of any group of n-cells to transform into r-cells. Complete realization of inherent potentiality for differentiation is here achieved, since the condition of physiological isolation implies the absence of all restraints on the processes taking place in the isolated system. Consequently, b may be taken as a measure of this inherent potentiality as evaluated in physiological isolation. In general, then, the ability to differentiate will vary directly with b, so that the larger the value of b, the greater is the potentiality for differentiation.

An important feature of this biological constant is that its value is obtained from a standard isolated state and as such is a characteristic of a group of cells independent of the environment in which they happen to find themselves. In this way, environmental modifications of differentiation potentiality can be considered separately. In a multicellular organism, b will vary from one group of cells to another, in general decreasing from the anterior to the posterior regions. It may here be stated that if physiological gradients are considered in terms of ability to differentiate, then the gradient in the constant b from point to point in the animal must be taken into account. We may call this parameter the "inherent differentiation potential."

Particular attention must be paid to the end process when differentiation is complete. To study this as well as the other parts of the transformation, it is sufficient to integrate equation (2) and observe what occurs when t is allowed to increase. Since two distinct variables are varying with t, equation (2) cannot be integrated directly. However, by means of (1) we may write

$$\frac{dR}{dt} = b(M - R) \tag{3}$$

This is integrated to yield

$$\ln C - \ln (M - R) = bt$$

where C is a constant of integration, the value of which is determined by the initial conditions. Passing to natural numbers, we obtain

$$M - R = Ce^{-bt} \tag{4}$$

For a general evaluation of C we may assume that at zero time, R, the mass of r-type cells has the value R_O so that

$$M - R = (M - R_O)e^{-bt}$$

For the special case being considered, in which the experiment is started with no r-type cells, R_O becomes zero and C reduces to M. For this case we may then write

$$R = \text{M}(1 - e^{-bt}) \tag{5}$$

Equation (5) gives the complete time course of the phenomenon. With increasing t, the exponential becomes smaller and subsequently becomes negligible, so that R approaches M in magnitude. When R reaches M, no further changes occur in the system with the passage of time. It is apparent that equation (5) predicts that the process of differentiation will stop only when all of the n-cells have transformed into the r-type. This, perhaps, can be more clearly seen from equation (3) where, unless b is zero, $\frac{dR}{dt}$ cannot become zero until R becomes equal to M in value, the total mass of tissue.

This prediction of complete potency realization is of course not surprising in complete physiological isolation, where no resistance to differentiation exists. However, a complete absence of environmental inhibition is of course rarely obtained, and a description more closely approximating reality would take such factors into account. In addition, greater generality and flexibility would be obtained by an analysis permitting some fraction of the total mass of cells originally present to remain undifferentiated. We may denote this fraction by

$$\epsilon = \frac{K}{M} \qquad (6)$$

where K is the mass which actually transforms into the r-type, $(M - K)$ remaining undifferentiated. The number ϵ varies between zero and one and is characteristic of a particular tissue under standard external conditions. In general, it will vary with changing environmental circumstances. Since it is a measure of the non-realization of potentialities due to environmental resistance, it may be called the "environmental coefficient of resistance." The situation described by equation (5) becomes then a special case where ϵ is unity and K is consequently equal to M.

There are further implications in equation (3) which would bear closer examination. The b in this equation is a constant and does not vary with time. No objections can be raised against this implicit assumption if all the cells transform simultaneously. However, if it is desired to examine a less restricted condition where various cells in the population take different amounts of time to complete the transformation, a serious difficulty arises. A time-independent b for this case would imply that the differentiation potential of the cells which transform later in the process is the same as that of those which did so earlier. This is patently untrue unless it is further assumed that the later ones are of greater mass or were stimulated to begin the differentiation at a later time. The acceptance of either of the assumptions as a complete justification would lead to a condition that does not seem biologically plausible, since it would suppose that in any group of cells, all possess precisely the same potentiality to undergo transformation. To a certain extent it is possible to avoid this difficulty by assuming that one can deal with an average b for the entire population of cells, admitting the possibility for variation of this parameter from individual to individual within the group. This particular approach will be adopted in the present discussion, as it proves to be a reasonable one. The further detailed analysis in terms of a distribution function for the b values is more complicated and will be reserved for a future study.

The assumption of an average b does not, however, solve the problem. There remains a difficulty of a peculiarly biological nature. From the constancy of b with time one must conclude that the differentiation of some portion of the group of cells has no apparent effect on the potentiality of the remaining undifferentiated ones. This is biologically unsound, for it in essence implies that each cell is physiologically isolated from the other members of the group as far as differentiation is concerned.

As has already been indicated in the general discussion of physiological competition, there are at least two ways in which the cells which have differentiated can influence the differentiation potentials of the remaining n-cells. Firstly, if the differentiation results in a change of metabolism, the new metabolites formed may prove harmful to the n-type cells and inhibit their transformation. Secondly, by their transformation they have decreased the amount of substrate available to the untransformed cells. Consequently, unless the available biological space and the rate of supply of the substrate are both above the critically limiting level, the appearance of each r-type cell results in a decrease of the differentiation potentials of the n-cells yet in existance.

If either or both of these two competitive inhibitory processes are operating, then, at any given stage of the transformation, it is necessary to decrease the inherent differentiation potentials of the n-cells present, by an amount proportional to the mass of r-cells formed in the past. There exist no exact criteria by means of which the precise quantitative law of this variation can be decided upon. All that is known is that it must express potential limitation as a function of R, the mass of r-type that has appeared. For the purposes of the present discussion, it is sufficient to examine a simple linear relationship. We may then write for the "actual potential," (b_t), of the n-type cells at any given moment the following expression:

$$b_t = b - \lambda R, \tag{7}$$

where λ is a constant and b denotes the inherent differentiation potential. Equation (7) may be considered as a first approximation of a more general expression containing the higher powers of R. It will be noted that at the beginning of the process, when R is small, the actual differentiation potential, b_t, approximates b. As the differentiation proceeds, however, and R gets larger, b_t gets smaller and smaller until it finally approaches zero when R becomes equal to $\frac{b}{\lambda}$. It is thus apparent that b_t is a differentiation potential that varies from moment to moment, since it is a function of R which in turn is a function of time.

From equation (7) it is apparent that the larger λ is, the greater is the inhibition of the potential by a given mass of the r-type. Thus, both from the method of its insertion and from its definition, λ is seen to be a measure of the effect of the transformation process on those cells of a group which have as yet not undergone differentiation. It may, therefore, properly be called the "coefficient of interaction."

It will be noted that both types of interaction, competition for substrate as well as for physiological space, have been combined into the single interaction coefficient, λ. From its nature it is evident that λ will vary inversely both with the volume of physiologically available space as well as with the rate of substrate supply. Insofar as its value is dependent on the direct competition for substrate, it is possible to deduce on physiological grounds the probable relation between λ and b.

At any given substrate level, the b value of a particular cell will depend on the ability, in terms of amount per unit of time, of the cell to use the substrate. This ability, or b value, may then be referred to the concentration of the enzymatic components which use the substrate and supply the necessary energy for the transformation. Thus, the higher the b value of a cell, the greater its content of the necessary enzymes. Whenever effective competition for substrate is occurring it is necessarily true that substrate concentration is the limiting factor governing the rate of transformation. Under these conditions the rate is determined by the product of the substrate and enzyme concentrations, i.e., T, the rate of transformation is given by

$$T = kES$$

where E and S represent enzyme and substrate concentrations respectively, and k is a proportionality constant. It is clear from the above relation that a cell with a high b value, corresponding to a high value for E, will be able to maintain a given rate of transformation at a lesser substrate concentration than a cell with a low b value. Consequently, as competition sets in, and the substrate concentration level begins to drop, the cells with the low differentiation potentials will be the most drastically affected. Further, if as seems reasonable, a minimal rate of energy supply is required for building up the necessary structures, the low b-value cells will be the first to cease active differentiation. On this basis it is necessary to conclude, then, that a general inverse relation exists between the inherent differentiation potential and the interaction coefficient of any particular cell, i.e., the higher the b, the lower the λ and vice versa.

A word may be interposed here about the relation between b_t and b, the inherent differentiation potential. b_t was introduced to approximate more closely experimental experience than was possible with a time-independent potential. However, it is not to be considered as a mere replacement of one expression by another more closely descriptive of the truth. The concept underlying b must still remain as part of the theory. The reason for this resides in the desirability of retaining some method for arriving at a measure of the intrinsic potentiality of the tissue, independent of environmental variation. The parameter b fulfills this function since it measures transformation capabilities in the complete absence of external limitations, whether they stem from the presence of other cells undergoing the same process in the neighborhood or from some unfavorable environmental element of a more inanimate nature. The retention of b as an environmental independent constant does not ignore external effects. On the contrary it permits their examination apart from the kinetic consequences of inherent variations in b. Unless a separation of this kind were made, it would be difficult to examine the consequences of gradients in b as distinct from the effect of environmental polarizations.

TRANSFORMATION KINETICS OF A PHYSIOLOGICALLY ISOLATED GROUP, THE MEMBERS OF WHICH ARE IN PHYSIOLOGICAL COMPETITION

The critical examination of the condition with complete absence of internal and environmental interaction permits a natural extension of the analysis to the case where some of the biologically implausible restrictions are removed. In particular, it is now possible to analyze the situation where:

1) Interaction obtains amongst cells within a group so that the differentiation potential at any moment of any given cell is affected by the number of cells which have already undergone transformation.
2) Environmental influences may be felt on the process of differentiation through ϵ, the environmental coefficient of resistance.

While environmental influences are of great importance, if they are uniformly applied their results need not be crucial for final development. If they are polarized so that a particular region of the group is more drastically affected than others, the environment could under such circumstances impose its own polarity on the developing structure. Extremely low values of ϵ will also make the environmental influences critical, since they could thus numerically overshadow the internal parameters and consequently dominate the course of development.

To study the kinetics of the differentiation with both cellular and environmental interaction, equation (3) must be modified to include these factors. The differential equation expressing the time-rate of appearance of the r-type now takes the form

$$\frac{dR}{dt} = b_t(K - R) \tag{8}$$

where K is defined by equation (6) and b_t by equation (7). Substituting for b_t its definition as given, we obtain,

$$\frac{dR}{dt}(K - R)(b - \lambda R) \tag{9}$$

As in the analysis of the previous differential equation, of paramount interest is the state of the system when transformation ceases and no further changes occur in the value of R. Such a condition is described when $\frac{dR}{dt}$ assumes the value of zero. As can be seen from equation (9), there are two values of R which will satisfy this condition. They are given by

$$R = K \tag{10a}$$

and

$$R = \frac{b}{\lambda} \tag{10b}$$

The first value characterizes the non-interacting case, or at least the one where no effective interaction exists amongst the transforming cells. The second presumably applies when competition occurs during the transformation. It is apparent however, from the existence of the two possible values for R that a positive non-zero value for λ is not sufficient to guarantee interaction effects. In order for potency limitation to emerge from the competitive interaction, it is necessary to demonstrate that under these conditions R will approach a value less than K. It is clear, then, that a necessary condition for the existence of limitation is that $\frac{b}{\lambda}$ be less than K. It may now be demonstrated that this condition is also sufficient, by showing that under this assumption R approaches $\frac{b}{\lambda}$ rather than K.

Since it is proposed to study interaction effects, a positive non-zero value for λ is assumed in the following. Returning to equation (9), transposing and integrating the result leads to

$$\frac{1}{b - \lambda K} \ln \frac{\lambda R - b}{R - K} - \ln C_2 = t + C_1 \tag{11}$$

where C_1 and C_2 are constants of integration determined by initial and final conditions. Passing to natural numbers, we obtain from equation (11)

$$\frac{\lambda R - b}{R - K} = C_2 e^{(b-\lambda K)(t+C_1)} \tag{12}$$

Solving for R yields,

$$R = \frac{b}{\lambda - C_2 e^{(b-\lambda K)(t+C_1)}} - \frac{KC_2 e^{(b-\lambda K)(t+C_1)}}{\lambda - C_2 e^{(b-\lambda K)(t+C_1)}} \tag{13}$$

Equation (13) represents a complete description of the transformation of R as a function of time. It is now necessary to inquire what happens to R as t increases indefinitely under the particular assumption that $\frac{b}{\lambda}$ is less than K. It will be noted that this assumption implies that

$$b - \lambda K < 0$$

Consequently, when t is very large in equation (13), the exponentials having negative exponents become smaller, and with increasing t approach zero. The second term, possessing as it does an exponential in the numerator, disappears completely. Of the first term only b and λ remain. Thus the

$$\lim_{t\to\infty} R = \frac{b}{\lambda} \tag{14}$$

which, since $\frac{b}{\lambda}$ is less than K, signifies interaction leading to potency limitation. It is then possible to state the following general theorem on transformation dynamics.

> *Theorem 1.* The necessary and sufficient conditions that a group of transforming cells fails to realize its full potentiality for differentiation are that its members be in physiological competition and that the coefficient of interaction λ be greater than $\frac{b}{K}$.

It is of some interest to investigate what the theory predicts for the time independent value of R if $\frac{b}{\lambda}$ is greater than K, i.e., would R still approach $\frac{b}{\lambda}$? Under this assumption

$$b - \lambda K > 0$$

and the coefficients of t in the exponents are all positive. The limit approached by R for increasing time in this case may perhaps be more readily seen if equation (13) is rewritten as

$$R = \frac{\dfrac{\lambda}{e^{(b-\lambda K)(t+C_1)}}}{\dfrac{\lambda}{e^{(b-\lambda K)(t+C_1)}} - C_2} - \frac{KC_2}{\dfrac{\lambda}{e^{(b-\lambda K)(t+C_1)}} - C_2} \tag{15}$$

Here it is observed that with increasing t, the first term of the right hand member disappears, since its numerator goes to zero, and the second term reduces to K after cancellation of C_2. Thus, we find

$$\lim_{t\to\infty} R = K$$

The results obtained on the consequences of the two inequalities may be summarized in the following two statements

1. If $\frac{b}{\lambda} < K$, $\quad \lim_{t\to\infty} R = \frac{b}{\lambda}$
2. If $\frac{b}{\lambda} > K$, $\quad \lim_{t\to\infty} R = K$

It is of interest to note here for later use that the same conclusions may be derived directly from the differential equation (9) under the assumption that $\frac{dR}{dt} \leqq 0$. If $\frac{b}{\lambda} < K$, then R cannot become greater than $\frac{b}{\lambda}$ for then $\frac{dR}{dt} < 0$. If $\frac{b}{\lambda} > K$, then R cannot exceed K for then again $\frac{dR}{dt} < 0$. Hence statements 1 and 2 follow.

It is thus seen that when two values of R exist which will make $\frac{dR}{dt}$ vanish, the value which is actually assumed in the steady state is always the lesser of the two. This is merely another way of stating that limitation effects must occur if the interaction is sufficiently severe to insure that λ is large enough to make the ratio $\frac{b}{\lambda}$ less than K.

It is not necessary for the main problem to pursue the examination of the characteristics of the isolated group any further. With the emergence of potency limitation as a consequence of inter-member competition, the analysis has been brought to the point where an extension can be made which will permit an inquiry into the questions of group interaction and its effects.

Group Interaction

In harmony with the analysis as it has proceeded thus far, we may state the central problems of group interaction in the form of the following questions:

1) How, in general, is the physiologically isolated case changed when the group is placed in physiological contact with another undergoing the same transformation?
2) Under what conditions will potency limitation emerge from the group interaction?
3) What role do gradients in 'physiological activity' play in the transformation kinetics of such connected groups?

The first question poses the primary problem whose solution is essential before the others can be answered. In essence it asks, how must the kinetic equation of a group be modified when it is physiologically connected with another one. To make the problem more concrete, consider the case of two masses of tissue, each capable of differentiating into the same structure when isolated. Let one be of mass M_1, with a differentiation potential b_1, interaction coefficient of λ_{11}, and a coefficient of environmental resistance ϵ_1. Similarly, the parameters describing the second group may be denoted by M_2, b_2, λ_{22}, and ϵ_2 respectively. If the two groups are unconnected, then for each may be written a differential equation similar to equation (9). We would then write

$$\frac{dR_1}{dt} = (K_1 - R_1)(b_1 - \lambda_{11} R_1) \qquad (16a)$$

$$\frac{dR_2}{dt} = (K_2 - R_2)(b_2 - \lambda_{22} R_2) \qquad (16b)$$

where as before,

$$K_1 = \epsilon_1 M_1$$

and

$$K_2 = \epsilon_2 M_2$$

Since it is desired to examine interaction effects it will be assumed in the following discussion that λ_{11} and λ_{22} are both greater than zero and further that $\frac{b_1}{\lambda_{11}}$ is less than K_1 and $\frac{b_2}{\lambda_{22}}$ is less than K_2. Under these assumptions, the steady state values of R_1 and R_2 will be determined by the second of the two factors in the right-hand members of equations (16a) and (16b).

It was earlier suggested that gradients were necessary but not sufficient conditions for the existence of regulatory behavior. This proposition is of such crucial importance to the whole problem of the implementation of gradients as directive agents in morphogenesis, that a more rigorous re-examination of the problem is desirable. This may be done with the aid of equations (16a) and (16b). For the purposes of discussion let us assume that the two groups described by these equations belong to the same animal, group 1 being anterior to group 2. Furthermore, a gradient in 'physiological activity' exists such that it decreases posteriorly, being highest at the most anterior end of the animal. This physiological activity, insofar as it refers to differentiation activity, may best be measured by b, the inherent differentiation potential. With above assumptions, then, b_1 is greater than b_2.

We may now ask whether the existence of this gradient in b has any consequences for the kinetics of the transformations in the two groups, as described by equations (16a) and (16b). To put the problem in more specific terms, we may inquire whether the activity of the more anterior group affects through suppression or otherwise the differentiation of the posterior one. The answer is of course in the negative. This is not surprising, since no condition of connectivity has been imposed on these equations. They are completely independent, and consequently each has a solution of the form given by equation (13). The complete suppression of the activity of group 1, so that $\frac{dR_1}{dt}$ would assume a value of zero throughout the period of observation, would have no effect on either the existence of a limiting value for R_2, nor the magnitude of this value. It is solely determined by the ratio $\frac{b_2}{\lambda_{22}}$ and contains none of the parameters or variables which describe the condition and kinetics of group 1. Similarly, nothing going on in group 2 could possibly exert any influence on the transformation of group 1. It can be logically deduced, then, that the existence of a potential gradient does not unequivocally imply dominance over or suppression of one group by the more active one.

As was stated earlier, if it is desired that the two groups interact, the crux of the problem will lie in the mechanism assumed for the interaction. Mathematically, it is necessary to replace the set of independent differential equations by a system of such equations, not all of which possess solutions independent of the others. There are many ways in which this can be accomplished. In general, it is sufficient that the equation of each group contain some function of the variable R of the other group (or groups) with which it is interacting. The particular function chosen will depend on the biological mechanism selected for the interaction. Examination of the biology of the situation makes the problem of choice a relatively simple one.

Essentially, physiological connectivity or interaction would imply that the production of an r-type cell in one group should somehow influence the ability of the n-type cells in the connected group to undergo differentiation. It will be recalled that in correcting the condition of rigid physiological isolation of the member cells within a group, essentially the same problem was encountered on a lower biological level. The isolation was removed by assuming that the production of every r-cell decreased the differentiation potential of all the remaining *n*-cells; this decrease being interpreted in terms of substrate utilization as well as the production of harmful metabolites, or in general physiological competition. It is readily seen that an extension of this type of interaction amongst cells within a group to one involving cells of different groups provides a simple mechanism for group interaction. It is certainly reasonable to suppose that two groups of cells, each differentiating into the same structure, producing the same metabolites, and drawing on the same substrate source would influence each other in the same general way as do two member cells of a group. This would necessitate the existence of some physical connection between the groups. Among other means this could be accomplished through a circulatory medium from which both groups could draw on the same supply of substrate and into which they could both pour their metabolic wastes. If this physical linkage condition is satisfied, then the production of an *r*-cell in either group would decrease the potential of all the *n*-cells, in both of them. In terms of the variables and parameter thus far employed, this would mean that every increase in R_1 would decrease not only b_1 but also b_2. Similarly, every increase in R_2 would decrease the inherent potentials of both groups. Under these circumstances the actual differentiation potentials for the two interacting groups will be given by

$$b_{t_1} = b_1 - \lambda_{11}R_1 - \lambda_{12}R_2 \qquad (17)$$

for group 1 and by

$$b_{t_2} = b_2 - \lambda_{22}R_2 - \lambda_{21}R_1 \qquad (18)$$

for group 2, where λ_{11} and λ_{22} have their previous significance, and λ_{12} measures the effect on the differentiation potential of group 1 of the production of *r*-type cells in group 2. λ_{21}, on the other hand, measures the effect on the differentiation potential of group 2 of the production of *r*-type cells in group 1. Both λ_{12} and λ_{21} may then be called the coefficients of *group interaction*. The differential equations describing the transformation kinetics of the two connected groups 1 and 2 than take the forms,

$$\frac{dR_1}{dt} = (K_1 - R_1)[(b_1 - \lambda_{12}R_2) - \lambda_{11}R_1] \qquad (19)$$

for group 1, and

$$\frac{dR_2}{dt} = (K_2 - R_2)[(b_2 - \lambda_{21}R_1) - \lambda_{22}R_2] \qquad (20)$$

for group 2.

Fundamentally, it is of interest to examine whether potency limitation due to group interaction is inherent in these equations. Ultimately it would be desirable to determine whether dominance of one group over the other is also a deducible consequence. To aid in the analysis of equations (19) and (20) the following assumptions are made:

(1) $\lambda_{12} > 0, \lambda_{21} > 0, b_1 > 0, b_2 > 0, \lambda_{11} > 0, \lambda_{22} > 0$

(2) $\bar{R}_1 > 0, \bar{R}_2 > 0$

(3) $\frac{b_1}{\lambda_{11}} < K_1, \frac{b_2}{\lambda_{22}} < K_2$

(4) $\frac{dR_1}{dt} \geqq 0; \frac{dR_2}{dt} \geqq 0$

Assumptions (1) and (2) insure group interaction effects; the former guaranteeing physiological connectivity, the latter differentiation activity in both groups. Assumption (3) allows equations (19) and (20) to reduce to the physiologically isolated case with effective intermember competition within each group when the two coefficients of group interaction, λ_{12} and λ_{21}, are both equal to zero. Assumption (4) implies that no net decrease occurs in the number of the *r*-type cells in either group, i.e., dedifferentiation does not occur. This last assumption also permits the use of the argument in small type on page 128 to determine the steady state values of R_1 and R_2; thus the analysis may be made with the differential equations.

As in previous cases the end point of the transformation in a particular group will be reached when its R attains a value which will make its $\frac{dR}{dt}$ vanish. Under the assumptions on equations (19) and (20) it is clear that the steady state values for R_1 and R_2 will be obtained by setting the second of the two factors in the right-hand members of equations (19) and (20) equal to zero. Denoting the steady state values of R_1 and R_2 by $\bar{R}_1$ and $\bar{R}_2$ respectively, we thus have

$$b_1 - \lambda_{12}\bar{R}_2 - \lambda_{11}\bar{R}_1 = 0 \qquad (21)$$

$$b_2 - \lambda_{21}\bar{R}_1 - \lambda_{22}\bar{R}_2 = 0 \qquad (22)$$

Limited Realization as a Consequence of Group Interaction

That potency limitation is an immediate consequence of group interaction may be directly deduced from equations (21) and (22). Solving for $\bar{R}_1$ in equation (22) we find

$$\bar{R}_1 = \frac{b_1}{\lambda_{11}} - \frac{\lambda_{12}\bar{R}_2}{\lambda_{11}} \tag{23}$$

Since λ_{11}, λ_{12}, and $\bar{R}_2$ are all greater than zero, it follows that $\bar{R}_1$, the steady state value attained when the groups are connected, is less than $\frac{b_1}{\lambda_{11}}$, the steady state value reached by group 1 in isolation, i.e., for $\lambda_{12} = 0$. Similarly for group 2, it is found from equation (22) that

$$R_2 = \frac{b_2}{\lambda_{22}} - \frac{\lambda_{21}\bar{R}_1}{\lambda_{22}} \tag{24}$$

Here again, since $\bar{R}_2$ is less than $\frac{b_2}{\lambda_{22}}$, potency limitation due to physiological connectivity of the two groups is exhibited.

Dominance and Gradients

In order to examine the question of dominance and the effect of gradients on the transformation kinetics of connected groups it is necessary to determine what relation $\bar{R}_1$ bears to $\bar{R}_2$. Thus, for example, should $\bar{R}_1$ prove to be greater than $\bar{R}_2$, one could conclude that group 1 is dominant to group 2. Whereas, if the inequality were reversed, it would follow that dominance relations are also reversed. An examination of the desired nature may be made by solving equations (21) and (22) for $\bar{R}_1$ and $\bar{R}_2$ in terms of the parameters. The solutions thus obtained for $\bar{R}_1$ and $\bar{R}_2$ are given by

$$\bar{R}_1 = \frac{\lambda_{22}b_1 - \lambda_{12}b_2}{\lambda_{22}\lambda_{11} - \lambda_{12}\lambda_{21}} \tag{25}$$

$$\bar{R}_2 = \frac{\lambda_{11}b_2 - \lambda_{21}b_1}{\lambda_{22}\lambda_{11} - \lambda_{12}\lambda_{21}} \tag{26}$$

It may be noted as a check on these last two equations that they correctly predict values characteristic of the non-interacting case for zero values of corresponding group interaction coefficients; i.e., when λ_{12} is taken as zero, $\bar{R}_1$ reduces to $\frac{b_1}{\lambda_{11}}$, whereas if λ_{21} is taken to be equal to zero, $\bar{R}_2$ reduces to $\frac{b_2}{\lambda_{22}}$. Both $\bar{R}_1$ and $\bar{R}_2$ involve all the coefficients of interaction as well as both differentiation potentials. It is clear, then, that several quite different situations may obtain as far as their relative values are concerned. Any difference which may exist between $\bar{R}_1$ and $\bar{R}_2$ may equally likely depend on their potentials, interaction coefficients, group interaction coefficients, or a combination of these parameters. The major interest of the present discussion demands an analysis of those conditions which are necessary and sufficient for dominance. It is consequently desirable to examine the above possibilities separately insofar as such an examination is feasible. A comparison of the relative magnitudes of $\bar{R}_1$ and $\bar{R}_2$ can be more readily made if equations (25) and (26) are rewritten as

$$\bar{R}_1 = \frac{b_1(\lambda_{22} + \lambda_{21})}{\alpha} - \frac{\beta}{\alpha} \tag{27}$$

$$\bar{R}_2 = \frac{b_2(\lambda_{11} + \lambda_{12})}{\alpha} - \frac{\beta}{\alpha} \tag{28}$$

where,

$$\alpha = \lambda_{22}\lambda_{11} - \lambda_{12}\lambda_{21}$$

and

$$\beta = \lambda_{21}b_1 - \lambda_{12}b_2.$$

It is evident from equations (27) and (28) that since all other terms and factors are the same, attention need be focused in the following only on the numerators of the first terms of the right-hand members.

Case 1. *Absence of Gradients in Interaction Coefficients.*

In this case, emphasis is placed on the consequences for the transformation of the various possible order relations between the b values. It is assumed that λ_{11} equals λ_{22} and λ_{12} equals λ_{21}. Under these assumptions, it is evident from equations (27) and (28) that the following statements are true:

1. If $b_1 > b_2$, then $\bar{R}_1 > \bar{R}_2$;
2. If $b_1 < b_2$, then $\bar{R}_1 < \bar{R}_2$;
3. If $b_1 = b_2$, then $\bar{R}_1 = \bar{R}_2$.

It is thus seen that dominance is a consequence of gradients in potential, absence of a gradient leading to the disappearance of dominance relations. The theory further specifies the direction in which dominance will occur. The above inequalities indicate that under the conditions being considered, the group with the higher potential will dominate the other.

Case 2. *Absence of Gradients in Differentiation Potentials.*

Here b_1 is assumed to be equal to b_2. Since the interaction coefficients and group interaction coefficients stem from the same physiological mechanism, these two parameters of any given group may be allowed to vary in the same direction. Thus we assume that if $\lambda_{11} < \lambda_{22}$, then $\lambda_{12} < \lambda_{21}$. This seems reasonable, since if, e.g., members of group 1 are affected less by the formation of an *r*-type cell than are members of group 2, the particular position occupied by the *r*-type cells should not reverse the order relation between the coefficients. While this assumption of direct relation between the two types of interaction coefficients is not necessary for the mathematical analysis, it is a useful one for several reasons. In the first place, such a relation is physiologically more plausible than complete independence. Secondly, the examination of all the possible permutations of the order relations between the four coefficients which a supposition of independence would necessitate hardly seems profitable at the present stage. The following statements may then be written with the aid of equations (27) and (28):

1. If $(\lambda_{22} + \lambda_{21}) > (\lambda_{11} + \lambda_{12})$, then $\bar{R}_1 > \bar{R}_2$;
2. If $(\lambda_{22} + \lambda_{21}) < (\lambda_{11} + \lambda_{12})$, then $\bar{R}_1 < \bar{R}_2$;
3. If $(\lambda_{22} + \lambda_{21}) = (\lambda_{11} + \lambda_{12})$, then $\bar{R}_1 = \bar{R}_2$.

Here again, dominance emerges as a result of a gradient. As is to be expected from the nature of the parameters, the dominant group in this case is the one which possesses the lower valued coefficients of interaction.

The third possibility, where no inequalities exist either between the differentiation potentials or the interaction coefficient, needs no detailed discussion, since it is clear from statements 3 of both cases that this leads immediately to equality between $\bar{R}_1$ and $\bar{R}_2$, i.e., absence of dominance.

The statements listed under cases 1 and 2 demonstrate that a gradient in physiological activity whether it be measured in terms of the potentials or interaction coefficients, is a *sufficient* condition for the existence of dominance. Is it a necessary condition? That is to say, does the existence of dominance phenomena necessarily imply the coexistence of gradients in physiological activity? This question has been raised several times in the literature of critical discussions of the relations between gradients and dominance. Within the confines of the present theory the answer is in the affirmative. To demonstrate this, it is sufficient to show that the order relations used as hypotheses may be deduced from the conclusions. Thus under case 1, it is clear from equations (27) and (28) that

1. If $\bar{R}_1 > \bar{R}_2$, then $b_1 > b_2$;
2. If $\bar{R}_1 < \bar{R}_2$, then $b_1 < b_2$;
3. If $\bar{R}_1 = \bar{R}_2$, then $b_1 = b_2$;

and under case 2 that

1. If $\bar{R}_1 > \bar{R}_2$, then $(\lambda_{22} + \lambda_{21}) > (\lambda_{11} + \lambda_{12})$;
2. If $\bar{R}_1 < \bar{R}_2$, then $(\lambda_{22} + \lambda_{21}) < (\lambda_{11} + \lambda_{12})$;
3. If $\bar{R}_1 = \bar{R}_2$, then $(\lambda_{22} + \lambda_{21}) = (\lambda_{11} + \lambda_{12})$.

Case 3. *Inverse Relation Between Gradients in Potentials and Interaction Coefficients*

The setting up of cases 1 and 2 as separate problems for analysis implies that the interaction coefficients may vary independently of the differentiation potentials. This situation is possible under certain special conditions, and it was thus of interest to examine the consequences of gradients in the interaction coefficients above. However, as was pointed out previously (see pp. 127–128), a physiological interpretation of the interaction coefficients would indicate the existence of an inverse relation between them and the group potentials. Symbolically this would mean that

(a) if $b_1 > b_2$, then $\lambda_{11} < \lambda_{22}$ and $\lambda_{12} < \lambda_{21}$;
(b) If $b_1 < b_2$, then $\lambda_{11} < \lambda_{22}$ and $\lambda_{12} > \lambda_{21}$;
(c) If $b_1 = b_1$, then $\lambda_{11} = \lambda_{22}$ and $\lambda_{12} = \lambda_{21}$.

With the aid of (a), (b), and (c), and equations (27) and (28), the following statements may be made:

(1) If $b_1 > b_2$, then $\bar{R}_1 > \bar{R}_1$;
(2) If $b_1 < b_2$, then $\bar{R}_1 < \bar{R}_2$;
(3) If $b_1 = b_2$, then $\bar{R}_1 = \bar{R}_2$.

Dominance thus follows as a consequence of gradients in *b* without further postulating any relations amonst the interaction coefficients, since they are fixed by the inverse relation they bear to the potential. This case thus confers, in addition to physiological plausibility, the advantage of being able to confine the discussion to one parameter. It is evident that in this case, as in the others, the existence of a gradient is not only a sufficient condition for dominance, but also a necessary one, since the following propositions are true:

(1) If $\bar{R}_1 > \bar{R}_2$, then $b_1 > b_2$;
(2) If $\bar{R}_1 < \bar{R}_2$, then $b_1 < b_2$;
(3) If $\bar{R}_1 = \bar{R}_2$, then $b_1 = b_2$.

The results of the present section may be summarized in the following theorems on transformations dynamics.

> *Theorem 2.* A transforming group physiologically connected to another group which is also actively differentiating will experience potency limitation.
>
> *Theorem 3.* A sufficient condition for the absence of dominance phenomena between transforming groups is that the coefficients of group interaction be zero.

Assuming positive non-zero coefficients of group interaction, the following theorems on dominance may be stated.

> *Theorem 4.* In the absence of gradients in interaction coefficients a necessary and sufficient condition for the existence of dominance is a gradient in differentiation potential; the group possessing the higher differentiation potential will dominate the other.
>
> *Theorem 5.* In the absence of gradients in differentiation potentials, a necessary and sufficient condition for the existence of dominance is a gradient in interaction coefficients; the group possessing the lower interaction coefficients will dominate the other.

Case 3, upon which all subsequent discussion will be based, yields

> *Theorem 6.* If the potential of any group is inversely proportional to its coefficients of interaction, then a necessary and sufficient condition for the existence of physiological dominance is that there be a gradient in differentiation potential. The dominating group is characterized by the highest potential.

EXPERIMENTAL INTERPRETATION OF THE COEFFICIENT OF GROUP INTERACTION

A positive value for $\lambda_{ij} (i \neq j)$, according to the particular mechanism chosen for group interaction, can only be assumed when there exists a physical connection between the two groups which would allow flow of material between them. Any experimental procedure that destroys this physical continuity would result in a zero value for λ_{ij} and hence in physiological isolation for group *i*. If group *i* were a low potential group, this would necessarily be followed by the disappearance of any regulative action by the dominant group over the now isolated region. On the other hand, if group *i* were itself the dominant group, its isolation would release the others to which it was connected from its inhibitory influence. Such isolation can be experimentally attained most obviously by sectioning, incisions, constrictions, or blocking a circulatory system if one exists.

There is, however, another method of attaining isolation which is inherent in the basic concept of physiological competition. The coefficients of group interaction stem from the same resistances to transformation as do the ordinary interaction coefficients. They will vary inversely as the physiologically available space, insofar as competition for biological space contributes to their value. The widespread ability of cells which do not normally transform, to differentiate in isolation, would presuppose that most, if not all, produce the required substrate. It must be concluded, then, that the amount physically available to any group is directly proportional to the total volume or mass of cells physiologically connected to it. The severity of the competition between the two groups should then depend on the total mass of tissues with which they have established connection. Thus, insofar as direct competition for substrate contributes to the value of λ_{ij}, the coefficient of group interaction, it will again vary inversely as the total volume of tissue connected to the competing groups. Consequently, if a sufficient volume were so connected, λ_{ij} could effectively be made zero, and the two groups could be spoken of as in physiological isolation.

This particular interpretation of λ_{ij} has certain well defined implications for the experimental attack on the problem of dominance, to which we shall return when we consider that phenomenon in the regeneration of hydranths in coelenterates.

The type of physical connection established for mass transport between two competing groups is of some importance in determining the magnitude of the coefficient of group interaction, whether direct or indirect competition or both are involved. An effective circulatory system will tend to decrease local antonomy and increase the coefficient of interaction between groups. The complete absence of a circulatory system, with a consequent dependence upon the limited effectiveness of diffusion, will weaken regulative activity stemming from this mechanism. Even relatively small separations may in this case lead to more or less complete physiological isolation of two groups.

PHYSIOLOGICAL DOMINANCE

The primary purpose behind the development of the theory was to see if, on the basis of a simple mechanism, the regulatory nature of normal morphogenesis could be logically deduced. To some extent the analysis has already achieved this goal. However, thus far in the discussion of dominance, reference has been made only to its presence or absence. It would be highly desirable if the theory were to permit a more quantitative examination of dominance phenomena. Unfortunately, too many experimental and theoretical problems remain unsolved for a completely satisfactory quantitative approach to be developed at present. However, it is possible to derive certain interesting relations which have the advantage of being comparable with data on hydroid regeneration and thus offer an opportunity for testing the adequacy of the theory.

It is evident that a quantitative definition of physiological dominance must involve the severity of the inhibition of the less active group. The extent of the suppression is basically determined by the steepness of the gradients in differentiation potentials as well as by the magnitudes of the coefficients of group interaction.

A semi-quantitative approach to the problem may be made from the fundamental equations for the actual differentiation potentials of two groups, i and j, in competition with each other. These are given by

$$b_{t_i} = [(b_i - \lambda_{ij}R_j) - \lambda_{ii}R_i] \qquad (29)$$

$$b_{t_j} = [(b_j - \lambda_{ji}R_i) - \lambda_{jj}R_j] \qquad (30)$$

Assuming that b_i is greater than b_j, the severity of the suppression or regulation of the transformation of the j-group by group i, reduces to the question of how soon b_{t_j} will reach a value of zero.

It is manifest that several different situations can arise here. If both groups start their transformations simultaneously, and both have a zero value for their respective R, then a complete suppression of the inhibited group cannot occur, in a mathematical sense at least. During some finite period of time, R_j must assume a finite positive value. From a practical point of view, however, if the value be small enough, it need not be detectable, and a zero value may be assigned to it This hidden kind of differentiation cannot in all cases be ignored. Especially is this true in experiments involving the measurement of the differentiation rates of inhibited regions after their release from the regulation of dominant groups by isolation procedures. It is possible that the acceleration sometimes observed in these experiments is only apparent and is made up in part, at least, of the early unobservable portions of the transformation.

Complete suppression can of course occur if at the outset of the transformation of the J-group, group i has already reached some value R_i such that

$$(b_j - \lambda_{ji}R_i) = 0 \qquad (31)$$

for if this be the case no r-type cells could form in group-j.

It is extremely interesting to examine the extent of the limitation experienced by a dominated group. Consider again two groups i and j competitively interacting, with group i being the dominating one. The steady state values attained by the two groups are given by

$$\bar{R}_i = \frac{b_i}{\lambda_{ii}} - \frac{\lambda_{ij}\bar{R}_j}{\lambda_{ii}} \qquad (32)$$

$$\bar{R}_j = \frac{b_j}{\lambda_{jj}} - \frac{\lambda_{ji}\bar{R}_i}{\lambda_{jj}} \qquad (33)$$

The extent of the limitation resulting from the interaction may be obtained from the difference between the above steady state values and those attained in physiological isolation, i.e., $\frac{b_i}{\lambda_{ii}}$ for group i and $\frac{b_j}{\lambda_{jj}}$ for group j. These differences are gives by

$$\overline{\Delta R_i} = \frac{\lambda_{ij}\bar{R}_j}{\lambda_{ii}} \qquad (34)$$

$$\overline{\Delta R_j} = \frac{\lambda_{ji}\bar{R}_i}{\lambda_{jj}} \qquad (35)$$

These last two equations demonstrate one of the most important characteristics possessed by the present formulation, viz., a direct relation between the potency limitations of the inhibited group and the differentiation level arrived at by the dominant one. Several interesting and experimentally valuable consequences are immediately deducible. In the first place, it would imply that the closer group i is to the completion of its transformation, the stronger is its regulative activity. Furthermore, it would predict that when the complete structure is finally formed, the severity of the inhibition of the j-group will be greatest, for then R_i has attained its maximum value. The significance of this prediction lies not only in the fact that it presumes a regulatory activity for complete structures, but perhaps even more important, provides a simple and concretely specified mechanism through which such structures can control transformation activity in other parts of an organism, though they themselves are not apparently engaged in active differentiation.

The prediction of maximal regulatory intensity from fully transformed groups would imply certain well defined *time relations* for the dominance intensity between competing groups. For example, suppose group i is stimulated to begin its differentiation first, and after a certain interval of time group j is started. Under these circumstances, group j, instead of beginning its transformation with a differentiation potential of b_j, possesses one decreased by $\lambda_{ji}R_i$ where R_i is the value arrived at by the i-group during the interval of delay. If the latter is sufficiently great, the j-group will not get very far along the path toward the formation of a finished structure. We may thus have a situation where the inhibited group would have a much severer limitation on its potency realization than if it were started at the same time as the dominant group.

The theory would thus demand a dependence of dominance intensity on the time relations between the developmental processes of connected groups, and particularly on the interval between the stimulations to activity. In general, the longer the period of delay to the stimulation of the less active group, the more intense will the dominance be. It is clear that a reversal of the time relations should lead not only to a diminution of the regulative severity of the lower potential group, but in addition, should result in its final disappearance, if the interval of delay were of sufficient length. Under favorable circumstances, provided the discrepancy between the b-values were not too great, a complete reversal of dominance relations should be thus obtainable.

An opportunity to test these as well as other conclusions is afforded by the data on hydranth regeneration which is considered in the following section.

APPLICATION OF THE THEORY OF COMPETITIVE INTERACTION TO THE PROBLEM OF HYDRANTH RECONSTITUTION IN COELENTERATES

The very early work by Driesch (1897), Child (1907), Morgan (1903), and others on hydranth reconstitution clearly revealed that there could be no question of either predetermined regions destined to form particular structures, nor of a fixed polarity. Their experiments demonstrated concisely and unequivocally that any level of the hydroid stem has the ability to regenerate a hydranth. Recent work on the same question (see, e.g., Child, 1929, 1932; Zwilling, 1941) has served to emphasize this basic finding. Equally clear, however, is the fact that under the conditions of normal development, only the apical or distal end produces this structure, the potentialities of the more proximal portions being suppressed.

As far as regulatory activity is concerned, it is sufficient for the applicability of the competition theory to any particular case that two conditions be satisfied: first, physiological connectivity; second, the existence of gradients in ability to differentiate. With reference to the first, it would be difficult to deny the existence of physiological interaction between two regions connected physically to a common coelenteron containing a circulatory medium. In connection with the second condition, it is interesting to note that graded difference in rates of differentiation were pointed out by both Driesch and Child in the early work cited. More recently, Barth (1938) made a quantitative study showing how the rate of regeneration varies with the level of the stem. A typical set of measurements are reproduced in Fig. 1. In these experiments the rates of differentiation were so measured that they give an estimate of mass transformed per unit of time. Care was also taken to avoid interaction between regions during the measurement, so that tne inherent rate of each level was obtained. The values can be associated with b, the inherent differentiation potential of the theory. The data demonstrate clearly that a real gradient exists in the ability to differentiate as measured by the rate of differentiation.

(*A*) *Experimental Conditions Leading to the Disappearance of Dominance*

A fruitful approach to the comparison of theory with experiment may be employed by noting whether the experimental conditions leading to the disappearance of regulation correspond to those deducible from the formulation.

In this connection we may examine certain experimental findings which when considered together present a more or less critical interpretive problem. *Tubularia* stems of intermediate length (from 5 to 10 mm.) display the familiar regulative behavior of the distal end over proximal reconstitution. However, short stems of about 1 mm.

in length do not show such distal dominance. Furthermore, the distal ends of stems 15 or more millimeters in length also lose their ability to control the differentiation of the proximal ends.

The loss of distal dominance in the two rather different experimental conditions cited above may be explained from the point of view of a competitive interaction between the two ends. In any potential gradient if any two points are taken sufficiently close together, the difference between them can be made vanishingly small. Thus the distal end of a short stem would lose its ability to regulate the regeneration at a proximal end simply because one of the necessary conditions for dominance, i.e., an effective gradient in differentiation potential, no longer obtains between the two groups. The discussion of the characteristics of λ_{ij}, the coefficient of group interaction, permits a relatively simple interpretation of the disappearance of dominance in the experiments with long stems. The physiologically connected volume, with which λ_{ij} varies inversely, has been made so large that these interaction coefficients have disappeared from the kinetic equations, at least insofar as they critically determine the end point in the transformations of the two groups.

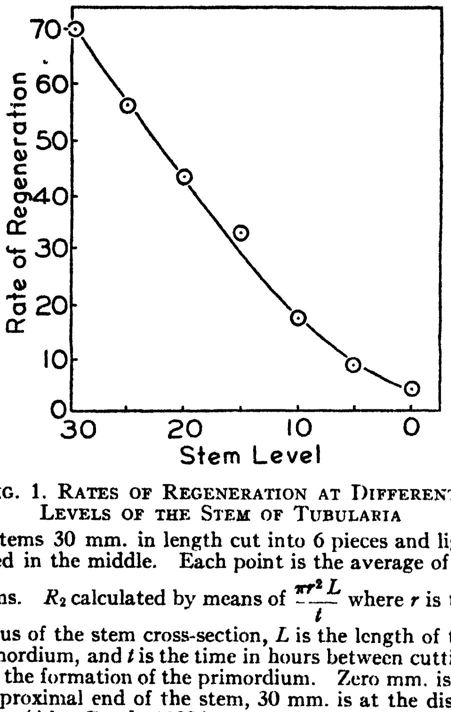

FIG. 1. RATES OF REGENERATION AT DIFFERENT LEVELS OF THE STEM OF TUBULARIA

Stems 30 mm. in length cut into 6 pieces and ligatured in the middle. Each point is the average of 10 stems. R_2 calculated by means of $\frac{\pi r^2 L}{t}$ where r is the radius of the stem cross-section, L is the length of the primordium, and t is the time in hours between cutting and the formation of the primordium. Zero mm. is at the proximal end of the stem, 30 mm. is at the distal end. (After Barth, 1938.)

The further examination of the concept of physiological connectivity as it applies to the particular organism in question leads to other interesting experimental methods for abolishing dominance. The essential condition of connectivity, implying as it does mass transport, must depend on a free access of the coelenteronic fluid from one group to the other. Thus, any interference with the free circulation of this fluid should lead to a parallel loss in the ability of the distal end to inhibit hydranth formation in the proximal portion of the stem. Such experiments have been done (Barth, 1938), blocking of the material exchange being produced by means of a ligature between the two ends. As is well known, treatment of this kind is invariably accompanied by a loss of regulatory activity in stems which would normally show it.

Experiments which use ligatures to obtain isolation of the distal and proximal halves are open to the obvious criticism that the procedure prevents not only the flow of fluid, but since the ligatures cut through the coenosarc, the transmission of stimuli is also hindered. To avoid this situation, prevention of material transport in the experiments of Barth (1938) and Rose and Rose (1941) was obtained by the injection into the coelenteron of either an oil drop or an oxygen bubble of sufficient size to stop fluid flow. The same disappearance of dominance relations was obtained in these experiments.

(B) *Experimental Modification of Transformation Kinetics*

An examination of the kinetic equations 19 and 20 for two competing regions shows that isolation (i.e., making λ_{12} and λ_{21} zero) should be followed by an increase in the rate of transformation. Data of this nature have been obtained by Barth (1938) for the coelenterate *Tubularia*. Rate was measured in terms of volume of hydranth formed divided by the time taken to arrive at a constriction between the primordium and the rest of the stem.

In choosing the experimental procedure to make the $\lambda_{12}R_2$ and $\lambda_{21}R_1$ terms disappear from the equations, it is important to avoid changing other factors than that of intergroup competition. Thus a ligature placed so as to divide the stem in two parts as shown in (b) of Fig. 2 effectively removes the possibility of distal-proximal competition, and consequently reduces both λ_{12} and λ_{21} to zero. However, at the same time the physiological space available to both groups is drastically decreased, resulting in proportionate increases in the coefficients of internal interaction, λ_{11} and λ_{22}. The net effect as far as resultant rates are concerned would under such circumstances be difficult to predict, since even decreases in rate might be obtained if isolation is produced in this manner. Indeed, such decreases would be expected providing the comparison is made with a very long stem in which all interaction coefficients are near zero, with the same kind of stems when the physiological space of each group is halved by a middle ligature. In an actual experiment in which 25 mm. stems were used, a ligature in the middle produced a 36 per cent decrease in the transformation rate of the distal half and about a 20 per cent decrease in that of the proximal.

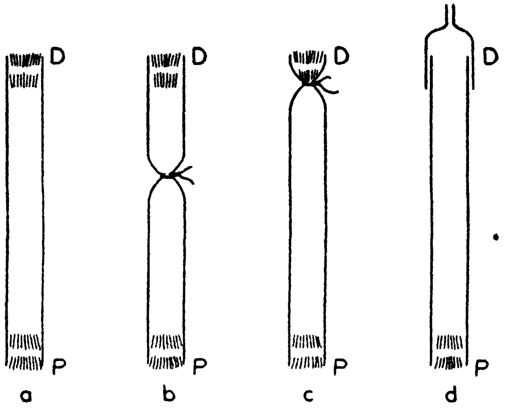

FIG. 2. EXPERIMENTAL CONDITIONS

P and D refer to proximal and distal ends respectively.
(a) Distal and proximal ends in competition;
(b) Isolation of the two ends (D, P) with a concomitant change in physiological space available to each;
(c) Isolation of the two ends (D, P) with little if any change in physiological space available to the proximal group;
(d) Isolation of proximal end obtained by inhibiting differentiation in distal end.

Focussing attention on the proximal group, which will be designated as group 2, a more adequate experiment would be to compare the rate of hydranth formation at the proximal end of (a) in Fig. 2 with that of the proximal end of (c) in the same figure. Here removal of the competition with the distal end is not accompanied by any significant changes in the physiological space available to the proximal portion of the stem. As can be seen from Table 1, experiments performed in this manner show a uniform increase in the transformation rates of the proximal ends over those obtained when the latter are in competition with the distal regions.

It will be noted that the method of ligaturing used in these experiments made the λ_{21} zero and thus removed the interaction term, $\lambda_{21}R_1$ from the rate equation. It is clear that another way of accomplishing the same thing would be to make and keep the R_1 zero, leaving physiological connectivity intact. As far as the quantitative effect on rate is concerned, the theory would predict that the same general increase would be obtained. Restriction of R_1 to a zero value can be accomplished by inhibiting regeneration at the distal end by means of a glass tube placed over it, as pictured in Fig. 2(d). In a typical experiment (Barth, 1938) the rate of regeneration of the proximal hydranth was 21.3 when the distal end was so treated, as compared with 4.0 and 2.7 when the former was in competition with an actively regenerating distal region.

TABLE 1

Comparison of rates of regeneration of proximal ends with and without competition with the distal end
(Barth, 1938)

EXPERIMENT	NO. OF STEMS	LENGTH IN MM.	RATE IN COMPETITION	RATE IN ISOLATION
A	6	5.0	0	36.8
B	14	7.5	0	31.9
C	14	7.5	3.9	15.1
D	10	10.0	10.7	35.9
E	10	10.0	4.4	13.0
F	10	10.0	0	8 6
G	10	13.0	41.7	53.0
H	10	13.0	17.9	28.1
I	10	15.0	12.6	26.8
J	10	15 0	18.8	20.4
K	10	20.0	19.0	28.9
L	10	25.0	29.0	47.4
M	10	25.0	27 9	34.0

It is of interest to see whether our particular interpretation of the coefficients of interaction is supported by the experimental data. Their existence as far as kinetic equations are concerned has the overall effect of decreasing the rates of transformation. Since they are presumed to vary inversely with the total physiologically connected volume, any increase in the latter, by decreasing the numerical magnitudes of these coefficients, should result in a general increase in rate. Such experiments can be performed by comparing the rates of differentiation of the proximal ends of stems under the conditions pictured in (b) and (c) of Fig. 2. In two typical experiments of this type, in which a total of 2.7 x $10^7\mu^3$ were added to the proximal end by moving the ligature distally a 50 per cent increase in regeneration rate was obtained, and in another the addition of 1.8 x $10^7\mu^3$ resulted in a 107 per cent increase.

These results have a certain critical value for the evaluation of the importance of physiological competition in the regulative mechanism of developmental processes. The fact that the competition hypothesis can predict rate variations in the transformation of an isolated group as a consequence of changing the amount of physiologically connected volume would appear to argue in favor of its playing a role in normal regulation. Indeed, it was experiments of this nature that first led to the invocation of competition phenomena as necessary for a more complete description of the facts (Barth, 1938, 1940).

EXPERIMENTS ON THE TIME COURSE OF DOMINANCE RELATIONS

In discussing the kinetic characteristics of physiological dominance, certain deductions were made directly from the assumption that the underlying mechanism was physiological competition. We shall in what follows see how closely they fit some available experimental facts. For the sake of simplicity in the comparison, they are listed in the following fashion:

1. A fully formed structure can regulate the extent of transformation of any lower potential region with which it is connected.
2. The intensity of the physiological dominance exerted by a group increases as it approaches the end of its transformation and attains a maximum value when the process is completed.
3. As corollaries to 2, the theory demands a dependence of dominance intensity on the interval between the stimulations to activity such that
   - (a) If the group with the greater potential is started first, the longer the interval to the onset of the transformation of the lower potential group, the greater will be the intensity of the inhibition of the latter.
   - (b) If no dominance exists between two groups, such can be made to appear by delaying the stimulation to differentiation of one or the other. By this means normal dominance relations may be reversed, and proximal groups made dominant to distal ones.

In an interesting series of experiments Watanabe (1935) presents data which offer the opportunity of subjecting the above conclusions to experimental tests. An ingenious experimental device allowed him to measure dominance intensity with relative ease. He employed pieces 15 to 20 millimeters in length from the distal stem regions of *Corymorpha* individuals. Such sections will almost invariably develop hydranths at both ends under normal conditions. By varying the conditions of the preparations of the stem sections, he could cause the suppression of either distal or proximal hydranths in these normally bipolar forms. Evidently the different preparation methods varied the dominance intensity of the two ends with respect to each other, and it was possible to measure the resulting changes in dominance by the frequency and kind of unipolar forms in the treated stems. The method had the added advantage that it measured the phenomenon in the whole range from zero to 100 per cent dominance.

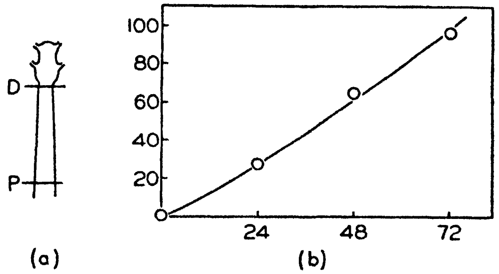

FIG. 3. REGULATIVE ACTIVITY OF AN ADULT HYDRANTH
(a) Experimental procedure. Proximal section at P at 0 hours; distal section at D at (0, 24, 48, 72) hours.
(b) Graph of results. Ordinates, percentage of unipolar forms; abscissae, hours; 50 pieces in each lot. (After Watanabe, 1935)

The basic idea behind the procedure was the employment of the delayed cut. Thus, in one series of experiments, a proximal section was made first at P (Fig. 3a), leaving the hydranth on the stem for varying lengths of time before it was removed by sectioning at D. This procedure, then, tests the ability of the fully formed hydranth to regulate proximal reconstruction. As is shown by the graph of the results (Fig. 3b), the frequency of proximal hydranth suppression rose uniformly from zero with no delay to almost 100 per cent when the delay of the proximal cut was about 72 hours. Aside from the direct verification of conclusion 1, the smooth rise of the dominance with the length of the delay is itself an interesting confirmation, for it would be expected that the longer the proximal portion is under the maximal influence of the complete structure, the severer the resulting inhibition would be.

Conclusion 2 and its corollary 3a are interestingly confirmed by the following experiment. Using the same kind and length of stems, a section was first made distally at *D* (Fig. 4a), and the proximal ones at *P* were made at various intervals after the initial cut. The data obtained are illustrated by Fig. 4b. It is immediately evident from the curve that the desired dependence of dominance intensity on the length of the interval of delay obtains during the course of development. The intensity rises quite steadily during the development of the dominant group, to attain a maximum value with the formation of a complete hydranth.

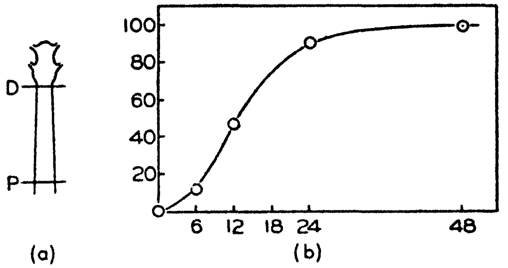

FIG. 4. INCREASING DISTAL DOMINANCE

(a) Experimental procedure. Distal section at D at 0 hours—proximal section at P at (0, 6, 12, 18, 24, 48) hours.

(b) Graph of results. Ordinates, percentages of unipolar frequency; abscissae, hours; fifty pieces in each lot. (After Watanabe, 1935.)

We may now turn our attention to some data which afford a test of corollary 3b, concerning dominance reversal. In particular, it is desired to test the implication that a suitable adjustment of the time relations could make a proximal group dominant to a distal one.

Using stems of exactly the same nature as employed in the previous experiments, simultaneous sections were made at *P* and D_1 (Fig. 5a). At various later times another distal section was made at D_2. The resulting new distal region, therefore, starts its transformation under the competitive influence of the proximal group at various stages of development. Figure 5b gives the data from an experiment of this type. It is clear from the curve that conclusion 3b is confirmed. As would be expected from the similarity of the kinetic equations for the two groups, this kind of reversed dominance follows the same upward trend with increasing delay of starting the distal group on the way to differentiation. However, it is interesting to note that the same 48 hour period of delay produced only a 63 per cent proximal dominance, whereas in the reverse case an almost 100 per cent distal dominance was obtained.

It would be desirable to repeat these experiments using the tube method (Fig. 2d) of inhibiting transformation activity. This would avoid disturbing the physiological volume relationships and would also have the advantage of keeping the same levels under study throughout the experiment.

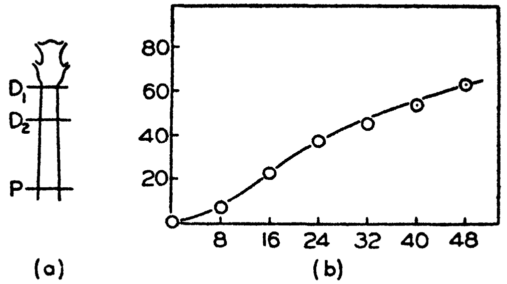

FIG 5. DEVELOPMENT OF PROXIMAL DOMINANCE IN CORYMORPHA

(a) Experimental procedure. Section at P and D_1 at 0 hours; second distal section at D_2 at (0, 8, 16, 24, 32, 40, 48) hours.

(b) Graph of results. Ordinates, percentage of unipolar forms at proximal ends; abscissae, hours. Fifty pieces in each lot. (After Watanabe, 1935.)

THE RELATION BETWEEN THE COMPETITION HYPOTHESIS AND THE FIELD CONCEPT

The development of competition as a regulative factor has depended rather heavily on gradients. Consequently, some answer to the problem of whether physiological competition can be incorporated into a field theory may be sought in the connection between gradients and fields. It is desirable to begin with a brief examination of the field concept as it has developed in physics, in which science the general abstract notion of a field has received its most complete development.

The physical concept of a field stems from the assumptions of the continuity of space and the indestructibility of energy. Further development along this line served to focus attention on the possibility of examining phenomena from the viewpoint of a physical continuum with the aid of field equations. There are in general two types of fields, vector and scalar. A vector field is one in which every point is associated not only with a magnitude but also with a direction. An example of a vector field is a field of force that may be defined as a continuous region of space at every point of which there is defined the force (in magnitude and direction) that would act on a standard particle placed there. Scalar fields are characterized by a numerical value at every point independent of direction. A potential field is a scalar field.

The connection between vector and scalar fields yields the desired relation between gradients and fields. The principle involved may well be illustrated by the simple example of a particle in a gravitational field. At every point in a gravitational field there is associated a gravitational potential which is defined as the potential energy per unit mass for a particle in the field. This potential is not only a function of the space coordinates but may also be a function of time if the field is nonstatic. In any case, however, the value at any given point in the region is not dependent on any particular direction and hence it is a scalar field. The most important characteristic possessed by a potential field is that the negative of its gradient is the force per unit mass, often designated as the strength or intensity of the field. Mathematically, if V denotes the potential and $\vec{F}$ the force or intensity, the latter is given by

$$\vec{F} = -\left(\vec{i}\,\frac{\partial v}{\partial x} + \vec{j}\,\frac{\partial v}{\partial y} + \vec{k}\,\frac{\partial v}{\partial z}\right) \quad .$$

with x, y, z being the coordinates and $\vec{i}$, $\vec{j}$, and $\vec{k}$ the unit vectors along the x, y and z axes respectively. It is clear from this equation that the simultaneous absence of potential gradients along the three coordinate axes implies the absence of force. Furthermore, it is physically meaningless to separate the force field from the gradients of potential.

A. The Biological Field

Essentially, what has been accomplished by the field concept in physics is the possibility for a unique description of the motion of matter in terms of the properties of space. The resultant field equations possess a characteristic unity, since only a single such equation is necessary for the description of the entire region. It is this unitary characteristic of the field theory which has impressed biologists with its possible utility for describing morphogenetic events. In adopting the term 'field' for biological usage, it was sought to emphasize the interconnection of morphogenetic events and the interdependence of the parts of the developing organism. Subsequent elaboration of these primary ideas has led to the field theory of development.

A brief description of a biological field may be presented in terms of the characteristics which it has been presumed to possess (Weiss, 1939; Huxley and de Beer, 1934).

1. A field is a spacial unity which is interrelated. The interrelation is expressed by the fact that events in one portion of the field have an important influence on events in other portions.
2. It is bound to a material substratum.
3. It is a pattern rather than a mosaic.
4. Such fields are characterized by quantitative gradients in regard to certain characteristics.
5. It is able to maintain its pattern within certain limitations when its mass is reduced and can perpetuate its pattern when completely divided into two or more pieces.
6. It is able to maintain its pattern when its mass is increased, and to fuse with similar patterns entering with the new material if the axial orientations are favorable.

It may be mentioned in passing that these six characteristics are not all logically distinct. This is true, for example, of 3 and 4. The assumption of gradients presupposes a continuity which would prohibit a mosaic pattern. The latter implies the existence of discontinuities and singularities which are not permissible within a field generally, though they may occur at its boundaries. In point of fact, a separate postulation of gradients is not logically necessary since the assumption of a field implies their existence (see below).

It will be noted that in the development of the biological concept of the field, insofar as the problem is considered, the main emphasis has been on the matter rather than the space. Thus we have a field whose "matter" can be increased and decreased. Little criticism can be leveled at the emphasis since, after all, the very data to be considered focus our attention on the morphology of the material rather than the space around it.

The failure of a close parallel evolution of the two has many reasons in addition to that already mentioned. One of the most important, which has seldom been clearly recognized, is the existence of a dichotomy in the problem of morphogenesis which prevents at once the direct application of the simple field concept. Morphogenesis consists not only of the movement of matter through space, which yields the changing form of the developing organism, but also involves the transformation of matter from one type into another, a process which has been named by some "chemical differentiation.'

Some conciseness in thinking could be gained if this were clearly recognized. The problem could then be reduced to some of its more elementary components, each of which may be simpler of solution that the composite picture they present. In addition, some of the incongruities which appear in the biological field concept due to the union of incompatibles would thus be avoided. If, for example, it was agreed to consider force fields and transformation fields separately, a logical segregation could be made of the characteristics mentioned on the preceding page. The force field would possess characteristics 1 to 4 inclusive, whereas the transformation field would be described by all six.

Some objections may be raised against this procedure, but it has its precedents in physics, in which science a single unified field theory is yet to be attained. The greater precision of definition possible would allow a closer and more exact examination of those fields which are more uniquely biological, i.e., the transformation fields.

Another advantage which may accrue from this procedure of separation is the development of a method of transfer from the physical to the component biological field. The inability to do so with the field concept as described by the six characteristics stems, as we have seen, from the attempt to lump all phenomena into a single biological field theory. This barrier is to a certain extent removed by the proposed segregation. The elimination of some of the physical inconsistencies permits the transfer of certain useful basic concepts. One such fundamental relation which may be mentioned is that between field and gradient in their most general sense, and about which some confusion has existed.

There has appeared at various times in the literature a curious schism between the so-called gradient hypothesis and the field concept. Certain authors, while not hesitating in their acceptance of the field concept, go to great lengths in their arguments against the existence of gradients. Other authors who accept both, do so on the "individual merits" of each. In still other cases the two ideas are combined in a fashion which would imply a separation that is not inherent in the field concept as it has thus far been understood and developed. Thus Huxley and de Beer (1934) state:

> "*Within these morphogenetic fields* various processes concerned with morphogenesis appear to be quantitatively graded so that the most suitable name for them is gradient systems or simply gradient fields." (Italics added).

Again, in a slightly later paper Huxley (1935) writes;

> "Such fields are always characterized *during certain* stages at least by quantitative gradients in regard to certain characteristics, and these gradients may be of various forms.

Other writers, in discussing the relative importance of the two, are even more definite in their implications that fields can exist distinct from gradients. Our discussion of the simpler physical field would deny this possibility since it showed a close and inseparable relation between the two. A field in which gradients are completely absent can effect neither the motion nor the transformation of matter and cannot therefore be invoked as a causal or descriptive agent for either. In the same vein it is meaningless to bring up the question (Needham, 1942) as to which is more fundamental, the gradient or the field? One may as well ask, which is more fundamental in determining velocity, distance or time?

One must admit that the relation between gradients and fields is not immutable. The two terms are, after all, words whose connotations may be altered at will. However, in those cases where such is the intent, a more explicit definition would be helpful.

B. Fields of Physiological Competition

To avoid unnecessary complications in the following discussion an inverse relation between the potential and interaction coefficients of a group will be assumed, as in Case 3. This permits an analysis which requires a knowledge of the potentials only, for determining the properties and subsequent behaviour of the system. In the preliminary development of competitive morphogenetic fields, the following questions will be kept in mind.

1. How many and which of the listed characteristics of a biological field do they possess?
2. Can they be more precisely defined than has heretofore been possible in the case of biological fields?
3. Does the theory provide a mechanism for interaction within the field?
4. In terms of the postulated interaction mechanism, can it provide a reasonable explanation why a field normally "realizes but a single actuality?" (This important question was raised by Huxley, 1935, in a discussion of the properties of biological fields.)

It is necessary at the outset to agree upon a unit, analogous to the test particle of physics, in terms of which we can both define a field and assess its qualitative and quantitative characteristics. The nature of this unit must ultimately be referable to the available experimental techniques if the theory is to have experimental consequences. Let us call this unit a 'group' and agree to mean by this term the smallest amount of material which can be experimentally handled. In some cases, as in blastomere experiments, the units will be simple cells. In others, as in many transplantation experiments in amphibian material, it will signify a group of cells. For present purposes, the only further qualification that is necessary is that no significant potential difference exist between any two elements of a group. Under such circumstances the conclusions are in general independent of group size.

Each group will be characterized by a set of parameters, among which we may mention differentiation potentials, coefficients of interaction, and coefficients of environmental resistance. In terms of these units, and the basic concept of physiological connectivity developed earlier, we may then set up the following definition of a field:

A field of physiological competition is a collection of physiologically connected groups.

Further development proceeds along the lines of a simple generalization of the considerations already met with the interaction of two groups. From the previous discussion it is known that a set of two equations is necessary for an adequate description of the interaction effects between two groups. Consequently a field such as has just been defined will not be described by a single field equation as in physics, but by a system of equations the number of members of which will correspond to the number of groups in the field. Thus, for n such groups, we would have:

$$\frac{dR_1}{dt} = (K_1 - R_1)\left(b_1 - \lambda_{11} R_1 - \sum_{i=1}^{n} \lambda_{1i} R_i\right)$$

$$\begin{array}{cccccc} \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \end{array}$$

$$\frac{dR_i}{dt} = (K_i - R_i)\left(b_i - \lambda_{ii} R_i - \sum_{\substack{j=1 \\ j \neq j}}^{n} \lambda_{ij} R_j\right)$$

$$\begin{array}{cccccc} \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \end{array}$$

$$\frac{dR_n}{dt} = (K_n - R_n)\left(b_n - \lambda_{nn} R_n - \sum_{i=1}^{n-1} \lambda_{ni} R_i\right)$$

In terms of these equations there exists the following precise, necessary, and sufficient condition that two groups by members of the same field:

> Two groups are members of the same field when, and only when, the dependent variable R_i of one appears in the differential equation describing the transformation kinetics of the other.

By the same token, we have for physiological isolation either one of two conditions:

(a) A group is physiologically isolated if its coefficients of group interaction with respect to all other groups are zero; or

(b) All the R's of all connected groups are zero.

While, as we have seen, the kinetic effects would be the same, the biological and experimental methods of arriving at the isolations defined by these two conditions are quite different. To distinguish them, condition (a) might be called "absolute isolation," implying a real physiological disconnection, whereas condition (b) might be named "effective isolation."

Not all fields defined by the above system of equations are functional in regulating the transformations of its member groups. It will be remembered that even with positive, finite values for both the λ_{ji}'s and the R_i's a gradient in potential is still necessary for regulatory activity. Analogous to the uni-dimensional case discussed previously we may then state in terms of the components of the gradients along the three coordinate axes x, y, and z, that a necessary condition for the existence of a functional field is that

$$\left(\vec{i}\,\frac{\partial b}{\partial x} + \vec{j}\,\frac{\partial b}{\partial y} + \vec{k}\,\frac{\partial b}{\partial z}\right) \gtrless 0$$

Non-functional or non-regulatory fields, given by changing the above to an equality, are of no interest in the description of organized morphogenesis.

In addition to the existence of potential gradients, there are certain other relations, derivable from the known properties of competitive interaction, which must obtain within a functional field. Let us define an iso-potential line as one along which the gradient in potential is zero. Similarly equi-potential groups are ones that have equal b values. The following characteristics of a competition field are then immediately deducible:

(a) No unilateral regulatory activity can occur between equi-potential groups.

(b) Dominance will not occur along iso-potential lines.

(c) Any field which has a potential distribution such that only one group possesses the maximum potential, will "realize but a single actuality" if all lower potential groups have values equal to (or very little greater than) the minimum amount of differentiation required for the realization.

(d) Within a single field multiple realizations will occur if more than one group possesses the maximum potential. Such maximal-potential groups, since they are equipotential with respect to each other, will complete the process without differential inhibitory interaction.

(3) Multiple realizations may occur in a field with a single maximum if some of the lower potential ones possess $\frac{\lambda_{ii}}{b_i}$ sufficiently above the critical minimum R_i value so that the regulation of the maximal group does not depress the steady state $\bar{R}_i$ of these groups below that minimum.

A pictorial representation of some of these characteristics may be obtained by plotting potential against distance from some arbitrarily selected axis. If it is desired to secure a two dimensional representation such that all the points in each distance-potential plane will belong to the same competition field, then a potential profile through the maximum may be made. Thus, with ordinates representing potential and the abscissae distance from the reference axis, Fig. 6a illustrates an unimaximal field and Fig. 6b one with two equipotential maxima at A and B so that both points realize their potentialities. The eye field in general, and in particular of the chick, investigated by Willier and Rawls (1935) is an example of one containing two equipotential maxima.

Without further analysis it is apparent from the above description that fields of physiological competition possess the important feature of the inter-relation of units. We may now briefly inquire whether they are also characterized by an independence from initial conditions implied by properties 5 and 6 listed in page 140. It must of course be realized that qualifying limits of reasonableness are imposed on this independence, for a certain minimal amount of tissue must be initially present to form a complete structure.

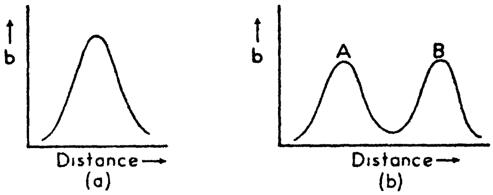

FIG. 6. DIFFERENTIATION POTENTIAL PROFILES THROUGH MAXIMA

(a) Field with a single realization.

(b) Field with multiple realization of equi-potential groups

The problem can most easily be examined by writing down the steady state value of R for a group i competing with a group j. Analogous with equation (25), this takes the form

$$\bar{R}_i = \frac{\lambda_{jj} b_i - \lambda_{ij} b_j}{\lambda_{jj}\lambda_{ii} - \lambda_{ij}\lambda_{ji}}$$

This expression contains none of the integration constants which are determined by the initial conditions. (Note that this is also true for the isolated group where the steady state value for effective competitive interaction is given by $\frac{b_i}{\lambda_{ii}}$. Thus unless the initial conditions are severe enough to express themselves indirectly through the interaction coefficients, the steady state values are independent of them. This more or less relative independence from initial conditions is a special case of a widespread phenomenon characteristic of all systems entering the steady state. Consequently, this property will be possessed by all transformation fields which require energy for maintenance. A more detailed examination of this interesting phase of the problem is beyond the scope of the present paper.

In addition to the above mentioned properties there exist certain general implications of the competition theory, as well as its field theory generalization, which are of importance to various other aspects of the general problem of embryogenesis.

Morphogenetic Plasticity

Since the theory predicts increasing regulative intensity in the course of the development of the dominant group, it is inevitable that the other members of the field lose their potentiality for transformations as long as they remain members of the field. Furthermore, since more than one field develops during morphogenesis within a limited space, it is unavoidable that those that developed earlier undergo contracture as the system evolves. The general trend during the evolution of the system is thus a rigidification of the component parts, both as to the space they can occupy, as well as to the transformation levels they can achieve as members of an organismic whole.

The same theoretical implications lead to an interesting interpretation of the onset of transformation in an established system. According to the theory developed, one of the critical factors which maintains the rigidity of the adult pattern is the existence of the dominant group which acts as a regulator in its adult form. Consequently, to induce differentiation in some other region of the field, it is sufficient to remove the maximal potential group. From this point of view then, the onset of the formation of, for example, a new hydranth in a coelenterate when the old structure is removed is mainly due to the removal of an inhibitory regulative activity. It is not necessary to postulate any specific stimulations due to cutting or other concomitant changes, though such cannot of course be ruled out. Such interpretations of the nature of regeneration in adult organisms are not new, having been admirably elaborated by Child (1941) and more recently by Rose and Rose (1941) in their experimental analysis of hydranth reconstitution in *Tubularia*.

Maintenance versus Morphogenetic Energy

Inherent in the basic concepts of the competition hypothesis, as well as in the above interpretation of the nature of the stimulation to regeneration, is the implication that the fundamental energy-yielding mechanism for the maintenance of an adult structure is intimately related to, if indeed it is not one and the same as, that utilized in its embryonic formation. A relation of this kind is difficult to deny in the face of the demonstrated ability of adult structures to control the constancy of organismic pattern. A plausible explanation may be made in terms of the utilization of a critical substrate. Experimentally, this would imply that a utilizable method of approach to the problem of, for example, the energetics of hydranth regeneration is the study of the adult hydranth itself and particularly those energy-yielding processes necessary to maintain its structural integrity.

The same viewpoint would also question the validity of recent attempts (see Needham, 1942, and Tyler, 1942, for discussions) to separate so-called 'maintenance' metabolism or energy from its morphogenetic counterpart. Thus, within the theory of competitive interaction it would be impossible to set up a definition of differentiation as "simply those processes not included under what we regard as maintenance."

We may cite an analogous situation in the growth of a population to make the point at issue clearer. When bacteria are seeded into a broth culture, it is well known that after an initial lag period, they enter into the exponential phase of their growth curve, which gradually tapers off as the population enters the stationary phase. It would be clearly meaningless here to set up a qualitative distinction of the energetics involved in the exponential period as compared with that involved in maintaining the population at the stationary level. The mechanism for keeping the population density constant is the production of new individuals to replace those that have perished. Thus the only difference between the exponential period and the stationary state of the growth curve is that in the former the rate of production of new individuals exceeds the death rate of already existent ones, whereas in the latter the two rates are equal. The fundamental energetics for the production of a new individual is the same no matter what part of the history of the population is being studied.

Precisely the same fundamental kinetic mechanisms are involved in the formation of a new cell or in the transformation of one type into another. It is undoubtedly true that "structural death" is continually occurring in a cell, necessitating a replacement mechanism. For the production of a new cell it is only necessary that the rates of syntheses of new structure exceed the normal rate of destruction. For its maintenance it is sufficient that they be equal. With each synthesis of a new structural unit there must occur a parallel qualitative and quantitative change in the "maintenance" energy required to keep the system at the new transformation level. Thus the energetics of maintenance and new syntheses become indistinguishable in nature except for a quantitative characteristic involving the difference between two rates.

There are other characteristics of these transformation fields which it is desirable to analyze. For example: precisely what does it mean to say that a given group of cells does not reach a particular transformation level but a lower one? Are all transformation levels realizable? In other words, does every point on the path of differentiation to a complete structure represent a point of sufficient stability such that the group will remain there if stopped? An examination of the problem from an energetics point of view would suggest an answer in the negative. A more likely situation would imply the existence of quasi-stable points, such that if a group found itself halted between two of them, it would go to one or the other, depending on the conditions of the energy flux rate. According to this concept, several quite different morphological and histological pictures could very well represent different levels along the same transformation path. And whether a particular group ends up in one rather than another would depend on its differentiation potential with respect to other members of the field.

In this connection mention may be made of Yamada's (1940) extremely interesting researches on the fate of chorda-mesodermal isolates of the salamander neurula. He found that presumptive blood islands, when isolated, yielded only blood island cells, but when a bit of notochord was included with the isolate, there resulted in addition to blood island cells, pronephros and some muscle. On the other hand, presumptive pronephros yields mainly pronephros and blood island cells. When, however, notochord is included in the isolate, muscle makes its appearance in 38 per cent of the cases. He was thus able to "raise" tissue "above" its prospective significance. He arranged the tissues in order of "morphogenetic potential" and interpreted his data in those terms.

However, such problems cannot be analyzed within the confines of the limitations imposed on the present analysis. An entirely different level of organization involving the energetics and points of stability of flux equilibria must be the basis for their adequate examination.

In summary, it may here be said that both the special and general properties found for the competitive transformation fields coincide in many ways with those of the biological field concept. The formulation provides reasonably precise definitions of fields and field membership, as well as an interaction mechanism in terms of which experimental consequences may be deduced. These are in general three-dimensional counterparts of those already discussed in the section on group interaction.

ACKNOWLEDGEMENT

The published work of Dr. L. G. Barth on hydroid regeneration served as the stimulus for the present analysis. My indebtedness to Dr. Barth is, however, even more direct. When the idea of elaborating a developmental theory along these lines was first proposed to him by the author, his immediate enthusiastic encouragement was the impetus that initiated it.

I should also like to take this opportunity to express my gratitude to Dr. H. B. Steinbach and Dr. V. Hamburger for their patient guidance during the various developmental stages of the manuscript and for very many helpful and suggestive conversations.

SUMMARY

An attempt has been made to develop a theory which would provide a regulatory mechanism for morphogenesis in terms of which potency limitation could be described.

Child's concept of physiological dominance has been examined, with especial attention focused on its logical relation to the gradient theory. It has been shown that an activity gradient *per se* has but limited explanatory usefulness unless it is implemented with an effector mechanism. Only then can dominance and other regulatory characteristics emerge.

A mechanism based on the competitive interaction of the transforming cells has been developed, several cases of graded biological complexity being examined. In terms of the theory, potency limitation was predicted, and its characteristics were examined. Precise conditions involving activity gradients have been deduced for the presence or absence of regulatory phenomena.

In terms of such parameters as differentiation potentials and coefficients of internal and group interaction, certain testable conclusions were deduced concerning transformation end-points and kinetics. In particular, the theory demands a dependence of dominance relations on the transformation levels arrived at by the various groups during the evolution of the system.

The above deductions and relations have been compared with available data on hydranth reconstitution in coelenterates.

The relation between the competition theory and the field concept has been analyzed. The examination permitted a rational generalization to a field theory of competitive interaction. The properties of such transformation fields have been compared with both physical and biological fields as they have been developed. The formulation permitted a reasonably precise definition of fields and field memberships.

LIST OF LITERATURE

Adelmann, A. B. 1929a. Experimental studies on the development of the eye, I. *J. Exp. Zool.*: 54, 249–290.

——. 1929b. Experimental studies on the development of the eye, II. *J. Exp. Zool.*: 54, 291–317.

Barth, L. G. 1938. Quantitative studies of the factors governing the rate of regeneration in *Tubularia*. *Biol. Bull.*, 74: 155–177.

——. 1940. Regeneration in hydroids. *Biol. Rev.*, 15: 405–420.

Boveri, Th. 1901. Über die Polarität des Seeigeleies. *Vhl. phys. Med. Geo. Würzburg*, 34: 145–175.

Child, C. M. 1907. An analysis of form regulation, I, II, III. *Arch. EntwMech. Org.*, 23: 396, 415, 445.

——. 1929. Lateral grafts and incisions as organizers in the hydroid, *Corymorpha*. *Physiol. Zool.*, 2: 342–374.

——. 1932. Determination of new axes by lateral graft and incisions in *Corymorpha* in relation to the gradient and dominance. *Physiol. Zool.*, 5: 593–627.

——. 1941. *Patterns and Problems of Development.* Chicago: University of Chicago Press.

Clarke, L. F. 1936. Regional differences in eye-forming capacity of the early chick blastoderm as studied in chorio-allantoic grafts. *Physiol. Zool.*, 9: 102–128.

Driesch, H. 1897. Studien über das Regulationsvermogen der Organism, I. *Arch. EntwMech. Org.*, 5: 389–.

Gurwitsch, A. 1922. Über den Begriff des embryonalen Feldes, Arch. *EntwMech. Org.* 51: 383–415.

Huxley, J. S. and de Beer, G. R. 1934. *The Elements of Experimental Embryology.* Cambridge, Eng.: Cambridge University Press.

Huxley, J. S. 1935. The field concept in biology. *Trans. Dynamics Devel.*, (USSR), 10: 269–.

Morgan, T. H. 1903. Some factors in the regeneration of *Tubularia*. *Arch. EntwMech. Org.*, 16: 125–.

Needham, J. 1942. *Biochemistry and Morphogenesis.* Cambridge, Eng.: Cambridge University Press.

Reiner, J. M., and Spiegelman, S. 1944. The energetics of transient and steady states. *J. Phys. Chem.* (in press).

Rose, M. S., and Rose, F. C. 1941. The cut surface in *Tubularia* regeneration. *Physiol. Zool.*, 14: 328–.

Schoenheimer, R. 1940a. *The Dynamic State of Body Constituents.* Cambridge, Mass.: Harvard University Press.

——. 1940b. The synthesis of protoplasm constituents. Second Symposium on Growth and Development. Growth (Supplement).

Spiegelman, S., and F. Moog. 1944. On the interpretation of rates of regeneration and the significance of the independence of mass and time. *Biol. Bull.*, 87: 227–241.

Spemann, H. 1938. *Embryonic Development and Induction.* New Haven: Yale University Press.

Thompson, D'Arcy. 1942. *Growth and Form.* 2nd ed. Cambridge, Eng.: Cambridge University Press.

Tyler, A. 1942. Developmental processes and energetics. *Quart. Rev. Biol.*, 17: 197–212; 339–353.

Watanabe, Y. 1935. Physiological dominance in *Corymorpha palma* in relation to reconstitution and methylene blue reduction. *Physiol. Zool.*, 8: 417–441.

Weiss, P. 1939. *Principles of Development.* New York: Henry Holt and Co.

Willier, B. H., and Rawls, Mary. 1935. Organ forming areas in the early chick blastoderm. *Proc. Soc. Exp. Biol. Med.*, 32: 1293–1296.

Yamada, T. 1940. Beinflüssung der Differenzierungsleistung des isolierten Mesoderms von Molchkeim durch Zugerfügtes Chorda and Neuralmaterial, *Fol. Anat. Jap.*, V. 19: 131–198.

Zwilling, E. 1939. The effect of removal of perisarc on regeneration in *Tubularia corcea*, *Biol. Bull.*, 76: 90–103.

MIMETIC POLYMORPHISM, A CONTROVERSIAL CHAPTER OF DARWINISM

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Preface

ABOUT fifteen years ago a small dinner party made up of J. S. Huxley, J. B. S. Haldane, A. R. Fisher, E. B. Ford, and the present writer met at the Athenaeum Club in London. I do not remember the topic of the conversation, but Haldane was preparing a book on the causes of evolution, Fisher had his well known book in press, Ford was to make a special study of mimetic polymorphism, and Huxley was to edit the *New Systematics* and to write a book on evolution in which mimetic polymorphism was to be treated in the light of the views of Fisher and Ford. If the conversation and discussion had turned to the topic of mimicry I should probably have stated my views similarly to the contents of the following paper. Had this been the case, it would certainly have been a lively, if not heated discussion, but nevertheless one among friends. In such a spirit the following critical discussion is presented.

INTRODUCTION

Ever since evolution became the central problem of zoology, students in this field have turned their attention to the wing pattern of Lepidoptera. Already Bates, Wallace, and Darwin had discussed the cases of apparent mimicry from the standpoint of selection; Müller continued the study of mimicry in Lepidoptera and found important principles, now bearing his name. Eimer used predominantly the pattern of butterflies as a basis for deriving his theory of orthogenesis. Weismann first started the study of experimental evolution in his work on temperature action upon the wing pattern of butterflies. He was followed by a whole school of experimenters, led by Standfuss, Fischer, Merrifield and Countess Linden (complete bibliography in Biedermann, 1912) who tried to solve phylogenetic problems in Lepidoptera by temperature experiments involving the wing pattern. All of these authors and their followers had the feeling, if not the conviction, that a considerable part of the secret of evolution lay hidden behind the manifold and beautiful patterns of Lepidoptera, and that an understanding of these patterns would constitute a large step towards the explanation of evolution. The present author, followed by Kühn, carried this conviction into the present era.

Among the many specific problems attacked was one which came to the foreground in many subsequent discussions: that of mimicry in butterflies, both in the form of mimicking the environment (e.g., leaves) and of mimicking other protected animals (e.g., wasps). In the latter group belong, as a specially interesting set of facts, those remarkable cases in which butterflies of one group mimic others belonging to another family whose members are supposed to be protected by poisonous juices or repellent taste. The interest in these phenomena, which had already been thoroughly discussed by Wallace and Darwin, was reawakened when the rising tide of Mendelism led to a new evaluation of selection. It was De Meijere (1910) who first furnished genetic information upon the subject; while Punnett (1915), whose student Fryer had succeeded in analyzing another case, took up a discussion of the whole problem from the viewpoint of genetics. Punnett's general conclusion was that selection of small mutants could not explain the origin of the genetic system involved in these cases. In a discussion of some problems of evolution from the standpoint of physiological genetics (Goldschmidt, 1920), I accepted Punnett's explanation and tried to point out some facts regarding pattern formation which I considered to be in favor of Punnett's viewpoint. Some years later a completely new point of view was introduced by R. A. Fisher (1927–30), derived from his general theory of the origin of dominance by selection of modifiers in the heterozygote A parallel idea was developed for the origin of the mimetic patterns. These ideas were taken up most enthusiastically by Fisher's former student, E. B. Ford (1936–40), who made special studies of the actual material in order to prove Fisher's point.

In all these discussions (with the exception of that in my book, 1920a) one decisive group of facts was completely left out of account, namely, that pertaining to the determination of wing pattern in butterflies. I returned to the subject (Goldschmidt, 1927) and tried to formulate a model of pattern formation in the complicated cases of mimicry, based upon Punnett's genetical interpretation and upon a generalized theory of genetical control of all patterns. In a recent paper, Ford (1936, p. 444) remarked that one element in my explanation, the track for the spread of melanin, does not conform to that actually observed in intermediates. Though my explanation was meant only as a model, not as a literal explanation, for which the data had been missing, Ford's criticism is justified in so far as I failed to take into account sufficiently the knowledge of pattern formation which was beginning to accumulate at the time of my writing. Actually a considerable body of factual information has been found since: descriptive and experimental embryological knowledge of the pattern and its determination (Goldschmidt and students, and especially Kühn and students); the comparative morphology of pattern (Schwanwitsch, Süffert, Kühn, Henke); experimental shift of pattern (Goldschmidt and students, Kühn and students); phenocopies in regard to pattern (Standfuss, Fischer, Goldschmidt, Kühn); the genetics of pattern elements (numerous authors, especially Cockayne, Federley, Ford, Gerould, Goldschmidt, Harrison, Onslow, *et al.*). Under these circumstances a renewed analysis of the entire problem seems of interest, especially as many evolutionists are not aware of most of the work, just mentioned, many geneticists are cognizant only of work done with their special pet animal or plant, and many embryologists are neither interested in insects or in genetical analysis. I feel encouraged to try such an analysis not only because I have myself performed experiments and done morphological work on many of the groups of facts involved, but also because I have considerable first-hand information on the other aspects, since, for example, Süffert's work on seasonal dimorphism and his comparative work on pattern was done in my laboratory, as was also Henke's elaborate work on pattern in Saturnid moths. I had, further, a chance to go carefully over the specimens from Fischer's famous temperature experiments and of Standfuss' breeding experiments (through the courtesy of Consul Biedermann in Zurich); I was able to observe in nature (in Java) some of the famous cases of mimicry and had the privilege of being shown by the late Professor Poulton his many boxes of families of *Papilio dardanus* upon which, later, much of Ford's work was based. Thus, what errors I may commit in the evaluation of the data are not based upon lack of first-hand information.

THE BASIC FACTS OF MIMICRY (MIMETISM)

A. Ecology

We shall not discuss here the ecological basis of our problem, i.e., the proofs that the mimetic forms actually mimic their model. If this were not the case, the entire problem would be only one of variation, without major importance for the understanding of evolution. The scholars who are mainly responsible for the elaboration of the principle of mimicry, Bates, Wallace, Darwin, Müller, and more recently, Poulton, and Carpenter have established the criteria for mimicry: relative scarcity of mimic as compared with numbers of model, rejection of the model by many predators, presence in the same locality and simultaneous flight. The data, collected by the best field observers, have been scrutinized many times. Not all points are perfectly clear, and there is a certain mass of non-conforming facts. But, as a whole, the mimicry theory stands the tests made, and the majority of trained observers, as well as theoretical evolutionists, accept the evidence. (For the most recent review see Cott, 1940, and Carpenter's discussion with Shull, quoted below.) There has been opposition to the interpretation as mimicry of the cases under discussion, as well as against the theory of mimicry as a whole (e.g., Heikertinger, Shull, Attee). But there are not many observers with field experience who belong to this group. Thus we accept the mimetic resemblance of the groups of butterflies under discussion as an established fact, but without denying that sometimes mimicry is claimed in rather dubious cases.

B. Simple and sex-controlled polymorphism

The typical cases of mimetism (as sometimes the special type of mimicry under discussion is called) are found in the following groupings:

1. Both sexes of a species of a butterfly are dimorphic. The best example (best, because genetic information is available) is ***Hypolimnas dubius*** Beau. from Africa, (Family Nymphalinae). On the west coast one of the two forms, ***dubius***, copies ***Amauris psythalea damoclides*** Stand., while the model of the other form, ***anthedon*** Doubl., is ***Amauris niavius niavius*** L. (Family Danainae). (The reader is referred to the condensed taxonomy of butterflies in Table 1, from which the relative systematic position of the groups mentioned here can be ascertained, together with the popular names of some typical species. Colored pictures are to be found in Haase's and Eltringham's monographs, Punnett's book and in Seitz's standard work.)

TABLE 1

Lepidoptera

(*after Kukenthal, 1936*)

- Superfam. Rhopalocera (Butterflies)
  - fam. Pieridae (whites)
    - subfam. Pseudopontiinae
    - " Dismorphiinae, e.g., *Dismorphia*
    - " Pierinae, e.g., *Pieris*, whites, *Colias*, yellows
  - fam. Papilionidae (swallowtails)
    - subfam. Baroniinae
    - " Papilioninae, e.g., *Papilio*, swallowtail
    - " Teinopalpinae
    - " Zerynthiinae
    - " Parnassiinae, e.g., Apollo butterfly
  - fam. Lycaenidae 2 subf. (blues, etc.)
  - fam. Rhiodinidae 2 subf.
  - fam. Nymphalidae
    - subfam. Danaidinae (almost all tropical)
      - tribus Danaidini, e.g., *Amauris*, *Euploea*, and monarch butterfly
      - tribus Tellervini
      - tribus Ithomiini, only neotropical, e.g., *Mechanitis*, *Ithomia*
    - subfam. Satyrinae (meadow browns, etc.)
      - 5 tribus
    - subfam. Nymphalinae
      - tribus Acraeini, tropical, e.g., *Acraea*
      - tribus Clothildini
      - tribus Heliconini, neotropical, e.g., *Heliconius*
      - tribus Nymphalini, e.g., *Argynnis*, fritillary

2. Only one type of male exists, it being non-mimetic. There are two types of females; either, one resembles the male and the other is mimetic, or both types of females are mimetic. Examples of the former are found in this country. The swallowtail ***Papilio glaucus*** L. has in its southern range a second female form of dark color which is supposed to mimic ***Papilio philenor*** L. The type form is called ***turnus***, the mimetic one ***glaucus*** (see fig. 1). The second type is represented by the African ***Hypolimnas misippus*** L. (Nymphalinae) where both types of females are mimetic; the female form ***misippus*** mimics ***Danais chrysippus***, the other, form ***inaria***, copies the ***dorippus*** form of the same model (Danaidae). In both cases the males, and, in the first example, the male-like non-mimetic females show the typical pattern of their group, which is very different from that of the model's group. This is also true of all other comparable cases to be mentioned.

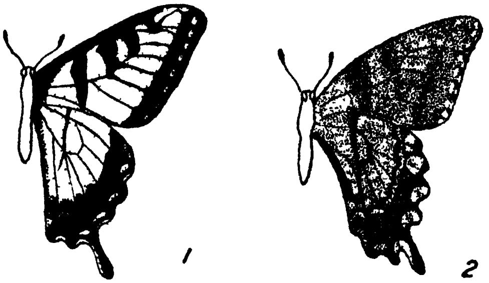

FIG. 1. PAPILIO TURNUS

1. ♂ (like non-mimetic ♀), ground color yellow.
2. mimetic ♀ *glaucus*, ground color except in wing margin blackish

Illustrations in black and white are rather unsatisfactory; they are not meant to replace colored figures but to serve as a crude help to the reader who does not know the actual specimens.

3. Only one type of non-mimetic male exists. There are at least three types of females: either, one like the male, non-mimetic, another different and non-mimetic, and a third mimicking a different species; or, there is one non-mimetic female with the same pattern as the non-mimetic male, and two different types of mimetic females, mimicking completely different species; or, all females are mimetic and mimic different models. The best studied and most frequently quoted examples of this type belong to the swallowtails (Papilioninae). One typical example is *Papilio memnon* L. of Java, with many female forms. Those used for analysis (Jacobsen and De Meijere) are the form *laomedon* Cr., non-mimetic and like the male; *isarcha* Seitz (formerly called *agenor*), also non-mimetic but different; and *achates* Sulzer, which mimics the protected *P. coon* F. In this case it is rather remarkable that the non-mimetic forms and the males are tailless, while the mimic has tails

like the model. A second comparable case is that of *Papilio polytes* Fabr., from Ceylon. One of the females resembles the male and is non-mimetic (*cyrus* Fabr.). The two other female forms are here mimetic. The form *polytes* copies *P. aristolochiae* Fabr., and the female *romulus* Cram mimics *P. hector* L. In this case all forms, including the model, have tails. It is to be noted that in this group the models belong to the same genus *Papilio*, but to a different section, namely Pharmacophagi or feeders on poisonous plants. (According to Haase (1891–93) Papilios fall into three groups: Pharmacophagi or poison eaters, who frequently possess warning colors and furnish the mimicry models; Cosmodesmus, which only in South America mimics poison eaters; and Papilio proper, which provides mimics of poison eaters as well as of completely different groups.) One of the most beautiful examples of South American mimicry is provided by *Papilio lysithous*, with six mimetic female forms (Jordan, 1911); but here no genetical data are available (see below).

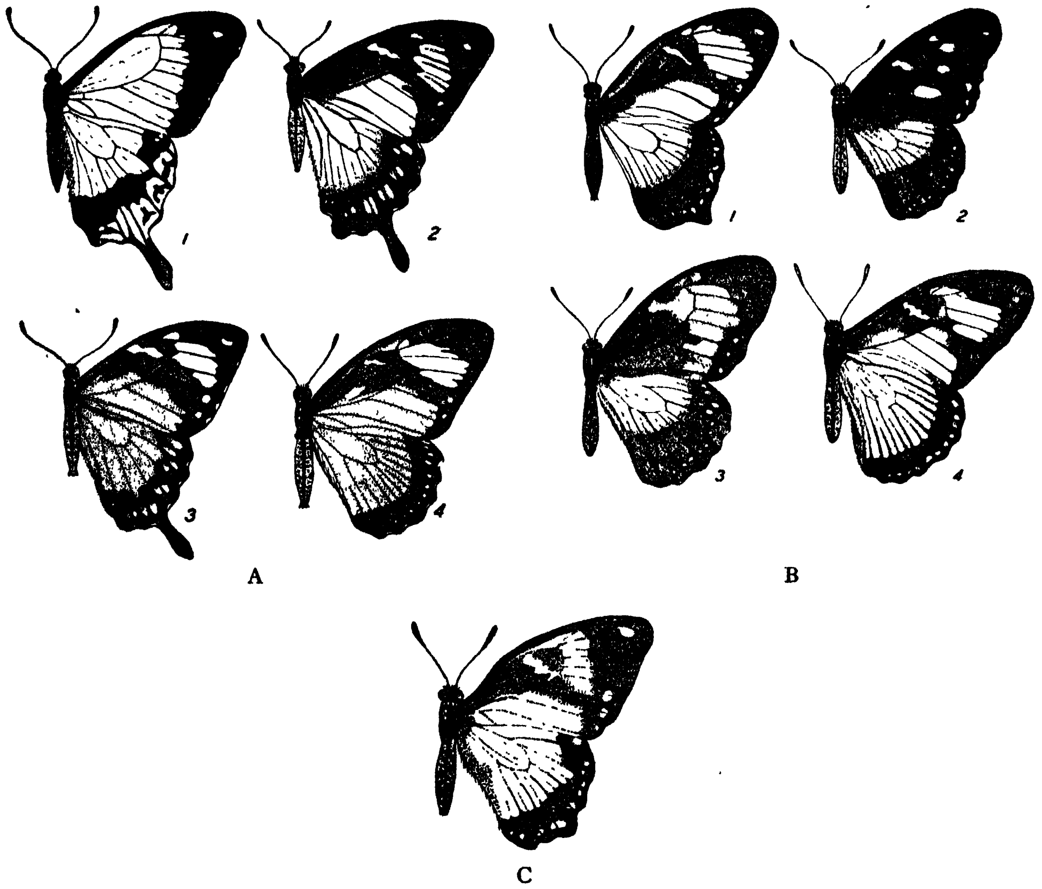

Fig. 2. Some of the Important Types of Papilio dardanus Redrawn from Colored Plates by Eltringham (1910)

A. 1. ♂ of *cenea*, also basic type of non-mimetic ♀, ground color yellow (fluorescent in ♂).
  2. *P. antinorii niavioides*, "tailed mimic," ground color white.
  3. *P. a. ruspinae* dto., ground color brownish, spots white.
  4. *P. d. trophonissa*, ground color forewings white, hindwings brownish.
B. 1. *P. d. hippocoon*, ground color white.
  2. *P. cenea cenea*, ground color hindwings yellowish (geogr. variety).
  3. *P. d. planemoides*, ground color forewings brownish, hindwings white.
  4. *P. d. dionysus*, not mimetic, ground color forewings white, hindwings yellowish.
C. *P. polytrophus trimeni*, proto-hippocoonides, ground color male yellow.

4. Again only one type of male exists. The females may contain different types in the different

races of the African *Papilio dardanus* Brown, which provides the examples for this group (see fig. 2). The females may be male-like, or different female types may be non-mimetic or mimetic and utterly different from the males; all female types may be different and mimetic or one type non-mimetic, the others mimetic. Also half-mimetic "pseudo" types are found. The models belong mostly to the groups Danainae and Acraeinae. Table 2 assembles a few of the types which were recorded by Ford, but the actually described forms are still more numerous (see Seitz, 1907ff., colored pictures in Punnett, 1915; Eltringham, 1910; Seitz; Ford, 1937; and many smaller papers from the Poulton school in *Trans. Entomol. Soc. London*, to be found in some libraries as collected contributions from the Hope Museum, Oxford). We shall return repeatedly to the types of variability visible in this table, which is based only upon the data used by Ford for his analysis.

TABLE 2

Mimicry in Papilio dardanus

(*See Fig. 2*)

HABITAT AND SUBSPECIES	NON-MIMETIC FEMALES	MIMETIC FEMALES	MODELS
Madagascar: *meriones*	one, with tails, like male		
Abyssinia: *antinorii*	one, with tails, like male	1. *niavioides*, tailed 2. *ruspina*, tailed 3. *wienholti*, tailed	*Amauris niavius?* *Danais chrysippus?* *Acraea jodutta?*
West Africa: *dardanus*	one different from male, *dionysus*	1. *hippocoon* 2. *trophonissa* 3. *niobe*	*Amauris niavius niavius* *Danais chrysippus* *Bematistes tellus*
Central Africa: *dardanus?*	—	1. *hippocoon* 2. *trophonissa* 3. *niobe* 4. *planemoides* 5. *cenea*	see above " " " " *Bematistes pogei* and others? *Amauris echeria*
North Eastern Africa: *tibullus*	one, *leighi*, rare, not malelike	1. *cenea* 2. *hippocoonides* 3. *trophonius*	see above *Amauris niavius dominicanus* *Danais chrysippus*
South Africa: *cenea*	the same	the same	
Mountains in Kenya District: *polytrophus*	like incomplete mimics, rudimentary tails, some male-like yellow pigment. 1. *protocenea*, i.e. between ce. and male 2. *protohippocoonides* 3. *prototrophonius* 4. *protosalaami* 5. *protoplanemoides*	1 *cenea* 2. *hippocoonides* 3. *trophonius* 4. *planemoides* 5. *salaami?*	see above " " " " " " " "

C. *Parallel geographic variation*

The foregoing table shows already that in *Papilio dardanus* geographic subspecies exist in which not only the males are different, as expected in geographic races, but also the mimetic females are more or less different, as their names indicate. These geographic differences involve the following phenomena: (1) existence or non-existence of male-like females; (2) occurrence or non-occurrence of non-mimetic females; (3) occurrence of mimetic females which copy in one region a model species not copied in another region; (4) occurrence of mimetic females copying the specific geographic variety of the model living in the region. In addition, different percentages of the respective forms are found in the populations inhabiting different regions. (Tables are found in Ford, 1937.) This parallels the well-known cases of other polymorphic species which have been discussed, more or less completely, in all modern books on evolution (see below). The most interesting feature is of course the parallel geographic variation of model and mimic. This phenomenon is also found in such other mimetic species as have not been mentioned thus far because less is known about them generally, and nothing about their genetics. It applies also to such mimetic forms as do not exhibit polymorphism. For the genetic analysis these are useless and have therefore not been mentioned thus far. Yet some of the most perfect examples of imitation belong in this group, e.g., the South American Pierid ("white") *Dismorphia praxinae* which copies the red and black striped (warning color!) Ithomiine *Mechanitis saturata* (see Punnett, 1915, plate X); the swallowtail *Papilio pausanias* copying the conspicuous Heliconine *Heliconius sulphurea* (Punnett, plate XI); or the amazing group of Asiatic cases like *Papilio clytia* and *xenocles* or the White *Pareronia ceylonica* copying Danaids of the most characteristic design (Punnett, plates I–III; other illustrations in color in Fisher, 1930; Haase, 1891–1893; Seitz, 1907 ff.).

D. Parallel behavior of sexual dimorphism

In the cases mentioned thus far, either both sexes are mimics and more or less identical or only the females are mimics of other groups without sexual dimorphism. Still more remarkable are the rare cases in which both mimic and model are sexually dimorphic, and the same dimorphism is found in both. Punnett (1915) mentions only two such cases. One is that of *Euploea mulciber*, a model of the Euploeine family, in which the male is brown with a deep blue suffusion, while the female is lighter, with less blue, and light streaked hindwings. A satyrid mimic of this, *Elymnias malelas*, has a similar sex difference! (pictured in Punnett, plate II). *Papilio paradoxus* mimics the same *Euploea* in the same way! These rare cases are important, as is the whole subject of sex related to mimicry. This will be discussed below.

The taxonomic names used in our presentation are those used by the authors to whom reference is made. Frequently they are not the names approved by the rules of nomenclature. The proper names may be obtained from Seitz. Names quoted from Ford, however, have been checked by this author.

E. Mimicry rings

Another important group of facts which has played a considerable role in evolutionary discussions is found in the so-called mimicry rings. This term means that there are species which serve as models not to one but to different species of different groups. Punnett (1915) illustrates a convincing case in colors (plate IV). The ring contains two species of Danaids (in this case both sexes) supposed to be distasteful, namely *D. chrysippus* and *plexippus*; further, the female of the Nymphaline *Hypolimnas misippus* (the male being very different); further, the females only of the Satyrine *Elymnias undularis* and of the fritillary *Argynnis hyperbius*, the latter two being considered as unprotected except by mimicry. Parallel cases are quoted in the writings of Poulton, Carpenter, *et al.* But decisive proofs are not always available of the occurrence of the prerequisites for mimicry (identical distribution, similar habits, etc.) in such cases.

F. Variability of mimics

In the theoretical discussion of the origin of mimetism the variability of mimics plays an important role, first, in regard to ecological relations and geographic coincidence of mimic and model, second, in regard to the phylogenetic origin of the protective pattern. We shall discuss many details below. Data concerning the descriptive facts are found in the papers already cited and in many others containing descriptions of so-called intermediate or primitive forms. Many of these have been given special names which can be found in the monographs of Seitz' opus. In this paragraph we record the facts only as a whole, not going into the details of pattern. The most conspicuous aberrations from the mimetic pattern are expected where the mimics imitate a very different form and therefore are very much different from the male form, which is generally supposed to represent also the original female form. The most important set of data is available for the African *Papilio dardanus* (fig. 2), data which have been assembled and extended by Ford (1937), who could use the huge material brought together by Poulton as well as that found in the great collections in England. As these data are an important link in Ford's discussion of the subject, we feel sure that he presented the facts rather completely.

1. Among the series of mimetic forms of *P. dardanus dardanus* is one, *dionysus* (see fig. 2b, *4*), which is considered to be non-mimetic. It has been described as either an intermediate between the mimetic female *hippocoon* and the non-mimetic female *meriones* or as a "reversal to an ancestral form." This type (to be discussed below) is considered to be very rare, not mimetic, and the black markings on the forewing vary from an almost male-like form to one nearly the pattern of the mimic. Another "rare nonmimetic form," in the subspecies *P. dardanus tibullus* and *P. d. cenea*, is the form *leighi* which combines some of the characters of the mimics *cenea* and *hippocoonides* with the mimic *planemoides*; the pattern of the forewing is somewhat variable (see fig. 2).

2. In the subspecies *P. d. polytrophus*, occupying the high mountain regions in the center of Tanganyika territory and parts of Kenya colony, an imperfectly developed mimicry is a typical feature. We shall discuss later Ford's explanation, which we state here in his own words: "Owing partly to the rarity in these mountain districts of the species which serve it as models elsewhere the various female forms so constant in other areas, are here exceedingly variable. Indeed they often show an approach to the ancestral male like forms." These imperfectly mimetic forms are distinguished by Poulton (1906), whom Ford follows, as "proto"-forms, independent of variety names given by taxonomists, e.g., proto-cenea including all varieties which may be described as imperfect *cenea* (see below and figs. 2, 9, 10). A proto-cenea looks like *cenea* but has the typical male yellow pigment which is absent in all typical mimetic females; proto-hippocoonides is intermediate in its black markings between the male-like female and the mimic *hippocoonides*, while male yellow pigment is usually present; proto-trophonius is more or less intermediate between the male type and the mimic *trophonius*. The black pattern varies as in proto-hippocoonides and white patches of *trophonius* are here male-yellow; *salaami* is a *trophonius* type in which white is replaced by orange to reddish brown; proto-salaami more or less resembles *salaami*, but the black pattern may be increased or considerably decreased and replaced by reddish ground. These types are considered to be non-mimetic. Proto-planemoides has a similar relation to *planemoides* as far as the black pigment is concerned. In this description of the proto-forms minor variations are omitted, such as yellow, fulvous, or white color of fore and hindwing spots (see below.) Collections from the district mentioned above include, according to Ford's count, 38 per cent of these proto-forms. *It is important to add that some of these abnormal forms occur as rare abberrations in other regions!* (For details, see Table 4.)

G. Genetics

It caused quite a stir among geneticists when De Meijere (1910) published the first genetic analysis of mimetic polymorphism in *Papilio memnon*, based upon Jacobsen's breeding results. This was a case of a *Papilio* in Java with one type of male and three types of females, one nearly like the male, and one of the other two copying a species of the Pharmacophagus group. In the original nomenclature the male-like female is called *laomedon* Cr., the non-male-like, non-mimetic female *agenor* L. (according to Ford it ought to be called *isarcha* Seitz) and the mimetic female *achates* Sulzer which copies the Pharmacophagus *P. coon* F. In this case all forms, including the male, are tailless except *achates*, which is tailed like the model. De Meijere realized that the breeding results can be explained on the assumption that all three female types are controlled by simple Mendelian differences. His detailed Mendelian explanation is now obsolete. The present author proposed (Goldschmidt, 1912) a somewhat different formulation which put the sex-controlled inheritance in the foreground and explained the situation as based upon two mutants of the alleles controlling the secondary sex-characters. A much simpler and now generally accepted formula was proposed by Baur (1911), which requires (in addition to sex-controlled inheritance) one dominant factor *A* which converts the female *laomedon* into *agenor* and a second factor *B*, which in presence of *A* produces the *achates* type.

Soon afterwards Punnett's student Fryer (1913) analyzed another case, that of the Ceylonese *Papilio polytes*, and he rather safely established the simple Mendelian relations between the forms. Following the old formulations of the Bateson school he represents the sex-controlled inheritance in terms of specific inhibitors, *Ii*. But I had already shown (Goldschmidt, 1912) that this type of heredity (the term sex-controlled was introduced only later by Goldschmidt, 1920b) is nothing but ordinary Mendelian heredity under control of the respective sex and its specific physiology of development. The specific inhibitors are thus superfluous. We remember that in *P. polytes* one type of female (*cyrus* Fabr.) resembles the male, another, *polytes*, mimics *P. aristolochiae* and a third, *romulus*, mimics *P. hector* L. The breeding results were explained satisfactorily by a dominant factor *A* which converts *cyrus* into *polytes*, and one *B*, which only in the presence of *A* converts *polytes* into *romulus*. Table 3 gives the formulae for all types of individuals.

Among the simple cases, with only two forms involved, some breeding experiments are available. This applies to *Hypolimnas dubius*, reported above as a form in which no sex-controlled inheritance is involved. On the basis of the breeding results obtained by Lamborn and Platt, Carpenter and Ford (1933) conclude that one of the mimetic forms, *dubius* or *mima* (geographic races) is produced by a single Mendelian dominant from the other (*anthedon*).

TABLE 3

Genotypes of forms of Papilio polytes

MALES ALL ALIKE	MALE-LIKE FEMALE CYRUS	MIMETIC FEMALE POLYTES	MIMETIC FEMALE ROMULUS
aaBB	aaBB		
aaBb	aaBb		
aabb	aabb		
AaBB			AaBB
AaBb			AaBb
Aabb		Aabb	
AABB			AABB
AABb			AABb
AAbb		AAbb	

What genetic knowledge is available regarding *Papilio dardanus* is mainly based upon the initiative of Poulton, who encouraged entomologists and fanciers residing in Africa to perform breeding experiments. Many individual reports have been published from the Hope Museum, some beautifully illustrated (mostly in *Trans. Entom. Soc. London*). The only geneticist to work over this material, much of which is preserved in the collections of that Museum, is Ford, whose detailed report (1937) we are therefore following.

The late Professor Poulton had, about twelve years ago, kindly granted me the permission to come to Oxford and to analyze his material; political events prevented me from taking advantage of his generosity. Fortunately Ford could still perform the work in Poulton's lifetime.

One of the basic difficulties emphasized by Ford is that most families were raised from captured females who might have been fertilized by more than one male. In addition the numbers look as if breeding was rather difficult and produced only small families, so that there is the possibility of differential mortality. The results cannot be summarized simply, as in the other cases. Actually, in the individual families obtained it cannot be decided with certainly which forms are dominant or recessive. Ford constantly had to refer to the percentages found in nature, which frequently do not fit properly the genetic results. Thus a detailed review is of not much use. The only statement which can be made is that, as far as the data go, one must expect a similar Mendelian situation for the major forms to that found in other polymorphic Papilios, as the families either consist of one or of different forms in what looks like Mendelian ratios.

It should finally be mentioned that there are indications of lethality or semilethality of homozygous dominants, (Carpenter and Ford) a fact observed also in other non-mimetic cases of sex-controlled inheritance by Gerould (1921) and by Goldschmidt and Fischer (1922). Ford is much interested in this point from the standpoint of selection in populations and discusses it in a recent contribution to *The New Systematics* (Huxley, 1940) (see below).

THE ORIGIN OF MIMICRY: PUNNETT VS. FISHER

Bates, Wallace, Darwin, and their successors Müller, Haase, Weismann, Marshall, and many others down to Poulton, discussed the origin of mimicry in general and of the special type which is under scrutiny here, from the standpoint of evolution by selection of small aberrations.

I should like to pay tribute to the memory of a great naturalist by mentioning that my interest in the subject was first roused when, as a young student (in 1901) I had the privilege to listen to a brilliant exposé of the subject by Professor Poulton.

Darwin himself did not fail to see the difficulties arising from the fact that selection can only work when a sufficient amount of resemblance between mimic and model has already been accomplished, sufficient to deceive the enemies. The genetic discoveries that such great differences as those between non-mimetic and mimetic females are based upon simple Mendelian factor differences suggested to Punnett a review of the whole subject.

Punnett (1915) first stated the case for warning coloration of distasteful forms and its imitation by mimics, as first observed by Bates in South America and therefore called Batesian mimicry; the classic models were later found by Wallace in Asia and by Trimen in Africa. Müllerian mimicry, i.e., mimicry between two distasteful forms, is treated as a special case. This, however, does not concern us here. After a detailed description of the best known cases of mimicry (a review which, together with Haase's classical work, 1891–93, can be recommended as a fair summary of the facts) Punnett offers his criticism of the classical theory of the origin of mimicry by gradual selection. Some of this criticism applies to the basic characteristics of any mimicry, as stated first by Wallace, i.e., occurrence of both forms in the same locality, harmless nature of the mimics, smaller numbers of them, considerable difference between the mimics and their next relatives, and purely external character of the similarity. Cases are mentioned which do not agree, and some of the rather wild explanations offered for aberrant facts are held up to ridicule. To mention only a few: The fritillary *Argynnis hyperbius*, supposed to mimic *Danais plexippus*, lives in the mountains while the model lives in the plains. The flight of such mimics as *Papilio clytia* or *Hypolimnas misippus* is completely different from that of their models of the Danaine and Euploeine group, and the same is true for non-mimetic as well as mimetic females of *Papilio polytes*. The mimics are not always completely different from their non-mimetic relatives, and the amount of difference found within the non-mimetic group is not smaller than that between mimic and model. In spite of such discrepancies the fact of mimicry is considered as established. But some of these discrepancies will enter the discussion of the origin of mimicry.

In the discussion of the origin of mimicry Punnett stated at the outset the two major possibilities: Either the resemblance has been brought about through the gradual accumulation of small variations by selection, or the mimetic form originated as a sudden mutation, and selection is responsible for its survival and for the destruction of the less adapted form. Fisher later called the second view origin by "saltation" and we shall therefore henceforth distinguish the two theories as the Darwinian or neo-Darwinian theory and the saltation theory.

The term saltation describes properly a large mutational step. I have spoken elsewhere (1940) of systemic mutation which however, implies a definite interpretation, namely intrachromosomal changes of a more complex nature than in ordinary mutation. Dobzhansky, in a critique of my views, has called them, unfortunately, a cataclysmic theory and this word has been repeated since by others as a kind of slighting label for unwelcome ideas. Cataclysma means deluge or catastrophe and thus does not convey the meaning of something involving only larger-sized causes and effects than assumed usually, but rather of something irrational and damnable. I must therefore object to the designation cataclysmic theory.

The first difficulty of the Darwinian theory, which was well known to Darwin himself, is the problem of the first step. If this does not produce a sufficient similarity with the model to deceive predators it has no selective value; but how can a small variation achieve such a minimum resemblance? Darwin and Wallace overcame this difficulty by assuming that originally there was only a small difference between mimic and model and that afterwards the present type was simultaneously built up in both. A powerful argument (already realized by Darwin) against this view can be derived from the so-called mimicry rings.

As already mentioned, it happens "that a given species in a given locality may serve as a model for several other species belonging to unrelated groups." In such a ring palatable and presumably unpalatable forms may be united. If now the Darwinian explanation of a slow accumulation of variations toward the warning pattern in both model and mimic, originally not very different, is applied, it follows that the ancestors of the members—e.g., one ring from Ceylon specified by Punnett as a Danaine *Danais plexippus*, a Nymphaline *Hypolimnas misippus* (here only the female is involved), a Satyrine, *Elymnias undularis* and a fritillary, *Argynnis hyperbius*—have been more or less alike. Such an idea would hardly appeal to anybody. This is still less the case if the sexual differences are also taken into account. Thus Punnett does not see any solution of such cases except by the saltation theory. He is also opposed to an intermediate view, that by a single mutation first a rough-hewn resemblance is brought about that is later perfected by selection of small variations. In his opinion this requires that selection continues operating, because otherwise the likeness would gradually deteriorate by regression. This is not considered to be the case.

Punnett's major argument is however derived from the case of *Papilio polytes*. Here quite a number of discrepancies in distribution, mode of flight, distinguishability of model and mimic have been observed. But here also the genetic analysis showed that simple Mendelian differences are responsible for the different types of females, as reported above. As such differences are only known to arise by single mutations, the mimetic resemblance must have been brought about in a single step for each type. (*It ought to be emphasized that neither in P. polytes nor in memnon was a single intermediate form found in the rather extensive experiments.*) Thus selection had nothing to do with the origin of mimetic resemblance though it probably worked in conserving it. Punnett discusses the latter point in detail, using the Hardy-Weinberg formula (see Stern, 1943, for this designation) for testing expectations in a population; in view of the persistence of a large percentage of the non-mimetic females over hundreds of generations, as judged from collectors' data, Punnett doubts that the mimics have much of a selective advantage. He mentions in this connection the case of industrial melanism, to which we shall return below, and also discusses the facts about the enemies of butterflies with which we are not concerned here, as our discussion presupposes the reality of mimicry.

Another important problem is discussed by Punnett: Even if mimetic forms originate by saltation, to use Fisher's term, selection will prevent establishment of new variations away from the mimetic resemblance. But in the absence of selection the resemblance will slowly be diminished or completely lost, an idea applied to actual cases especially by Carpenter (1913). Carpenter's famous example is that of the Nymphaline *Pseudacraea eurytus* mimicking the Acraeine genus *Planema*. On the mainland of Africa (Uganda) three mimics are found imitating perfectly three species of *Planema*, the latter being more abundant than the mimic in agreement with Wallace's rule. On Bugalla Island, however, the models are rather rare and the mimics abundant, and here many more transitional forms (as illustrated in many photographs) are found than on the mainland. (The parallel case of *P. dardanus* will be discussed below.) In this case little of the genetics is known except that different forms can be derived from eggs of captured females which makes it probable that the genetical aspect will not be much different from the cases already studied. Punnett suggests that the intermediates are heterozygous in some factor for which the typical form is homozygous, which would explain simultaneously the large number of intermediates in the population. The last word would be left to a future genetic analysis.

Punnett finally discusses some of the facts relating to parallel geographic variation. He does not enlarge upon such cases, as mentioned above, in which well known models and mimics show a parallel geographic variation. He uses, moreover, as an example a group of South American butterflies with warning colors which might constitute a mimicry ring or might not. Whether mimicry is involved or not, the fact remains that a series of "species" (probably subspecies or geographic races according to present-day notions) exists in different localities which show typical differences in pattern; and these differences run completely parallel in members of the families Heliconinae and Ithomiinae (more details below). Punnett makes the suggestion (since proven to be correct in other cases of geographic variation independent of mimicry, e.g., by the present writer for *Lymantria dispar*) that the new color scheme was associated with some physiological peculiarity which was advantageous to the individual in its new surroundings and was therefore selected. The same thing could happen in a parallel way in different species. (Again known to be the case in other groups, as the much discussed rules of Bergmann, Allen, Gloger, etc., in mammals and birds prove; see discussion below.)

In drawing his conclusions Punnett introduced still another genetical interpretation. He started with the fact that cases of mimicry tend to run in series, i.e., that a closely related series of mimics tends to resemble a closely related series of models, e.g., in Africa Papilios of the Cosmodesmus group mimic Danaid and Acraeid series. Thus the majority of cases of mimicry belong to one or another of such series as mentioned. "The natural interpretation of such phenomena" (Punnett) would be that in each group of Lepidoptera involved certain pattern factors are present, the permutation of which would produce the variety of patterns. Some of these factors (genes) may be common to two or more groups and thus make for similar patterns of unrelated forms. As a parallel case the coat color genes of different rodents may serve (Punnett); one could actually say that in some respects the rabbit mimics the mouse, in other features the guinea pig. With such a parallelization agrees the fact (always according to Punnett) that widely different models of different mimetic females of a species are related among themselves; it does not occur that one female form mimics a Danaine and another a poison-eater *Papilio*. If the explanation thus offered is correct, there would be available, among the possible pattern permutations of one group, combinations resembling those in another protected group. In this case a simple mutation of the basic color (e.g., harmless white into warning red) would at once produce the mimetic resemblance. But Punnett does not tell us how this scheme, which works theoretically between one *Papilio* and one *Danais*, etc., could be applied also to cases with three different kinds of females of completely different patterns.

If I am not mistaken, not many *geneticists* discussed the problem of the evolution of mimicry at that time, taking sides for or against Punnett. Actually the problem, one of the oldest and most important in evolution, is not even mentioned in such recent neo-Darwinian books on evolution as the excellent treatises of Dobzhansky and Mayr, though Shull, in his text (1936), largely follows Punnett, as far as genetics is concerned and goes even beyond him in his general criticism of mimicry (see Shull, 1937, vs. Carpenter, 1937). The present writer tried to set this problem into a definite place within his ideas relating to genetics and evolution and asserted (1920a) that the general trend of Punnett's ideas could hardly be refuted, though some points in detail require reconsideration. It was R. A. Fisher (1927, 1928, 1930) who took up the problem again from the Darwinian point of view in some papers preliminary to his well-known book, a work which is, to a large extent, responsible for the upsurge and present prevalence—almost a fashion—of neo-Darwinism.

Fisher was led to this problem by his well-known theory of the origin of dominance by selection of modifiers in the heterozygote. His basic concept is that selection acts upon the gene complex, modifying the response of the organism to the particular factor in question which itself remains unchanged. Rare genes will exist almost exclusively as heterozygotes. If they are disadvantageous, those individuals will be favored whose gene complex interacts to bring out the effects of the gene in question to the least degree, and vice versa in case of beneficial genes. Thus the tendency for characters to become dominant by plus selection of dominance enhancers (or to become recessive by the opposite selection) is spread through the species, while the existence of recurrent mutation allows repeated experience of genes acting in either direction.

One of the consequences of this idea is that the basic activity of a gene may be completely unaltered while selection acts upon modifiers for the phenotypic end effect. Statistically speaking, the selection of modifiers will be especially rapid in polymorphic forms because here the heterozygotes are still more plentiful than in the simple case. If this argumentation is applied to the facts of the genetics of mimetic polymorphism, the following explanation follows (Fisher, 1927): When any mutation produces by chance "*a remote resemblance*" to a more protected species, from which some advantage, however small, might be derived, the deception will constantly be improved by selection. This, working upon genotypical variability (i.e., on the whole residual heredity) will result in a gradual change in the effects of the gene concerned. Thus the effects will become very different from what they were at first. But the gene itself is unchanged and remains as a switch, turning on one or another set of characters subject to genotypic variability and thus susceptible to selection. Thus, though the forms of a species may be controlled by a single factor difference, which must have originated suddenly by mutation, we are nevertheless entitled to regard them as the product of slow evolution. (This review of Fisher's viewpoint has made use of literal excerpts from Ford, 1936, 1937.)

In presenting his idea of a switch mechanism, Fisher (1927) uses sex determination as an illustration, a comparison which Ford (l.c.) and Huxley (1943) accept. Fisher argues: "The core of Punnett's argument in favor of the production of mimetic forms by saltations lies in the Mendelian behavior of the polymorphic females, for it is argued that these Mendelian factors must have arisen originally as mutations, and seeing that the different forms demonstrably differ by only single factor differences, these types must have sprung into existence each at a single leap. Convincing as this argument at first sight seems, we should, nevertheless, at once recognize our folly if we argued that because the sex difference in *Lebistes* is apparently determined by a single factor, therefore a female fish of that genus with the appropriate adaptations of her sex had arisen by a single saltation from a male of the same species! [*Sic!*] Or vice versa. In this case we are freed even from the necessity of rejecting the supposed saltation as improbable, for since the reproduction of the species requires the cooperation of both sexes, we may be certain that the origin of the sex factor antedated the evolution of separate sexes, and has persisted, in its function of switch, unchanged during the whole course of the evolutionary development of these two types. The example of sex emphasizes strongly the fact that it is the function of a Mendelian factor to decide between two (or more) alternatives, but that these alternatives may each be modified in the course of evolutionary development, so that the morphological contrast determined by the factor at a late stage may be quite unlike that which it determined at its first appearance. The inference (on mimicry) requires, in fact, the gratuitous assumption that no evolutionary change has taken place in the two alternative forms since the dimorphism was first established."

Another comparison used by Fisher is that with the inheritance of pattern in hooded rats. The hooded pattern is a simple Mendelian recessive to self color. But a series of modifiers control the amount of color from almost dark to almost white by extension or restriction of this pattern, and these modifiers can be selected, thus producing selection of plus and minus patterns (Castle, 1919). Fisher ends this argument by saying that "unless the above analogies are wholly misleading" the alleles *A* and *B* (or *H* and *R* in Fryer's terminology) in *P. polytes* can be supposed to have arisen by mutation and remained what they were; but that there is no reason to believe that the combinations *AAbb* or *AABB* resembled at their first appearance the present types of swallowtail of these formulae. The selection of modifiers produced the mimetic types only afterwards. Once produced they are kept up in definite ratios because such stability is based upon the selective advantage of the actual ratio of the alternative types. Different such stabilizing actions are possible, one of them being reproductive selection of lethality of certain combinations (both of which have been observed, the first in *P. polytes* by Fryer (1913), the second in cases of sex-controlled dimorphism without mimicry by Gerould (1921) in *Colias* and by Goldschmidt and Fischer (1922) in Argynnis).

In a number of publications (1936, 1937, 1940a, b) Ford took up the problem of polymorphism and fully accepted Fisher's ideas. He added some new arguments based upon his own work, the most important of which are the following:

Fisher's use of the example of the hooded rats is followed up by a study of comparable genetic situations in Lepidoptera, which are used for a comparison with the mimicry cases. Ford himself (1940) studied crosses between *Abraxas grossulariata* (currant moth) and a yellow variety *lutea* distinguished by a simple Mendelian factor. F_1 is more or less intermediate and F_2 segregates in a bimodal curve. By selection it is possible to shift the degree of color in the heterozygote as well as in the homozygote. This must be due to the presence of modifiers which influence the phenotype within an ordinary monohybrid segregation. The selective change in the heterozygote may, of course, also be described as a shift in dominance in agreement with Fisher's view. (In *Drosophila* dominance modifiers are well known and have been made the subject of a special analysis by the present author under the name of dominigenes, see Goldschmidt, 1938a.) The parallelism to Castle's hooded rats is self-evident. As another example Ford quoted Federley's work (1920) on *Spilosoma lubricipeda* and its melanistic geographic race *zatima*. The heterozygote is intermediate, but by selection of modifiers it can be shifted in both directions. The homozygotes show much less effect of the modifiers than the heterozygotes, a fact which Ford considers important from the standpoint of Fisher's theory of dominance. (Details will be discussed below.) Both these examples are used as a genetic comparison upon which to base Fisher's explanation of mimicry.

In Ford's discussions the existence of intermediates between the mimics and non-mimetic females of different mimetics plays a considerable role. Actually he considers this phenomenon as a potent proof of Fisher's theory. Thus we learn of the case of *Hypolimnas misippus* L., where two types of females copy *Danais chrysippus* and *dorippus* respectively. The two mimetic females (*misippus* and *inaria*) are based upon an unifactorial difference, as already stated, *inaria* being recessive. Rare intermediates between them occur in nature and Leigh (quoted from Ford) bred from one such. He obtained a family of 8 females (sic!) of which 4 were *misippus*, 3 *inaria*, and 1 intermediate. From this Ford concludes that the intermediates have a genetic basis and adds: "Here then is an instance of genetic variability within the expression of a single gene in a mimetic species. It is of precisely the type required by the theory. . . ."

Ford has made a special study of the intermediates in *P. dardanus*, where they are described (aside from the taxonomic names given to them by collectors) as "variability" of the main types or as "incompletely developed" forms. They appear as rarities in the different races mentioned above, but, as already reported, are rather frequent in one subspecies, *polytrophus* of the highlands around Victoria Nyanza. They are considered so important because in this region the models are supposed to be very rare. Therefore, it is assumed, selection for the mimics has more or less ceased, and thus the modifiers may change the type without selective punishment. It must be emphasized that here the incompletes are something different from the intermediates in the last mentioned example. "Indeed they show often an approach to the ancestral malelike forms. This may be recognized in three ways. First the amount of black pigment on the wings is often reduced. Secondly females with rudimentary tails are sometimes found. Thirdly they may possess a certain amount of the yellow pigment of the male, present also in the malelike females of subspecies *meriones* and the *antinorii* group, but never in the females of the other races. . . ." To this must be added that the male yellow pigment is fluorescent in ultraviolet light (Cockayne, 1924), while no other pigments, even of the same color, show this phenomenon. Some of these incomplete females have been described above (proto-trophonius, etc.). More details will be found in Table 4 (see also figs. 2, 9, 10).

TABLE 4

Incomplete forms of P. dardanus, compiled from Ford, 1937

(See Fig. 2)

TAXON. NAMES	LIKE INCOMPLETE FEMALE	PATTERN	PIGMENT
Swynnertoni Poulton *mixtus* Aur. (proto-planemoides)	*planemoides*	Orange bar on forewings interrupted by black	Base of hind wings pale yellow (instead of fulvous)
Dionysus Doubl. (only in *P. dard. dard.*)	*hippocoon*	Area on hind wings enlarged, black markings, forewings variable, sometimes reduced to almost male type	Area hindwings pale yellow instead of white
Proto-cenea	*cenea*		Some male yellow pigment
Trimeni Poulton, *dionysoides* Aur. together: protohippocoonides	*hippocoonides*	Intermediate to male-like females	± male pigment
Lamborni Poulton (proto-trophonius)	*trophonius*	Black markings forewings variable, orange area restricted	Male pigment in all areas white in *trophonius*
Poultoni Ford *dorippoides* Trim. (proto-salaami)	*salaami*	Black markings increased or decreased ±	Small spots in forewings yellowish or white (instead of reddish brown)

There is relatively much information available on the genetics of these incompletes, though Ford states that it does not seem possible at present to draw definite conclusions, with one partial exception. It is fairly sure that all these forms are genetic and that they are inherited *on rather simple lines*. Each form appears significantly more often among the progeny of its own type of female than among those of the other varieties. It seems that the proto-forms are recessive to the full form, assuming that they are based upon genetic modification of the same allele. One result obtained from a controlled mating (which alone excludes mating with more than one male) is remarkable: A wild *cenea* female had produced 13 *cenea* and 7 proto-cenea. One *cenea* and two proto-cenea were mated with brothers. The first female produced 7 *cenea* and 1 proto-cenea; one proto-cenea produced 5 proto-cenea and 8 proto-trophonius; the other one produced 4 proto-cenea. (Ford thinks that the ratio 8:5 is significant for an expectation 3:1; but according to Warwick's tables it is highly insignificant for all ratios up to 15:1; the 7:1 ratio is insignificant for all possible ratios, and so is the 4:0 ratio. In my opinion no conclusions can be drawn from the ratios except that only two types are segregated.) The proto-salaami form gave rather comparable results, namely offspring: either only proto-salaami, or proto-salaami and *hippocoonides* in a significant 1:1 ratio, or proto-salaami and proto-trophonius.

There is finally one important result: *poultoni* is a small deviation from the proto-salaami type, but intermediates exist. A brood from such an intermediate contained all transitions between *poultoni* and proto-salaami, which, however, means only, judging from Ford's plate, small variations in the completeness of a dark band (see fig. 9).

"Intermediates" have also been recorded in other cases of polymorphic mimicry. Thus in the North American *Papilio glaucus* the yellow non-mimetic female (*turnus*) is supposed to be recessive (Cockayne, 1932) to the mimetic dark form *glaucus* (model *P. philenor*). But intermediates occur, and "these are probably due to a failure in dominance" (Ford, 1937).

It is to be noted that Ford, though emphasizing the importance of the intermediates and "incompletes," does not derive any detailed genetic conception concerning these forms. He states only on different occasions that "they (the intermediates) do, however, represent precisely the type of variation which we are here postulating as providing a basis upon which selection may bring about gradual evolutionary change."

A third major topic in Ford's argument against Punnett's theory of saltation is his criticism of Punnett's idea that the mimetic resemblance might be explained on the basis of parallel mutation (see above, p. 156). Ford emphasizes (with Fisher) that one of the most consistent features of mimicry is its superficiality (Fisher had mentioned different insects imitating ants and other such types of mimicry). Though the patterns of model and mimic may be extremely alike in their general appearance, they are nearly always distinct in their detailed marking, the similar colors seem often to be produced by different pigments or in a different manner. Thus Ford concludes (1937): "When we find apparent similarities between models and mimics constantly dependent upon devices of a fundamentally different kind, it is impossible to regard them as due to parallel mutation. It may also be mentioned that such a view necessitates a corollary which I believe few workers would be willing to accept: that the differences (e.g., in pattern and color) between dissimilar, and often not closely allied, species are themselves unifactorial if copied by a mimic exhibiting unifactorial polymorphism."

Ford believes that a powerful argument in favor of such views may be derived from his studies on the chemistry of wing pigments. He finds (1927, 1940) that red pigments in Lepidoptera are generally of two types: A, which is converted by strong mineral acids into bright yellow and returns to red in alkali; B, which turns into dull bluish after treatment with acid. It turned out that the models of the Pharmacophagus group in the swallowtails have pigment A while the mimics have B (e.g., in the *P. polytes* case).

Finally, it may be mentioned that Ford offers also an interpretation of the fact that frequently mimics copy the specific geographic form (subspecies) of the model characteristic for different regions. (Examples have been mentioned before.) Without going into details Ford asserts that it may be supposed that selection, operating on the gene-complex, has adjusted the effects of the same factor to the needs of the different races.

Thus Fisher's and Ford's arguments against Punnett's interpretation may be summarized in telegraphic style: 1. Intrinsic improbability of sudden emergence of the mimetic pattern. 2. Availability of a neo-Darwinian conception of evolution by selection of modifiers (derived from Fisher's theory of origin of dominance). 3. The simple Mendelian basis thus would apply only to a switch reaction. 4. Genetic models for such a situation exist, namely inheritance of sex, of color in hooded rats, and some examples in Lepidoptera. 5. The relative numbers of mimics and models agree with selectionist expectations. 6. These expectations agree with facts indicating a greater variability of mimics where models are rare. 7. Parallel geographic variability is best explained by selection of modifiers. 8. The existence of intermediates is a proof of the presence of many otherwise invisible modifiers. 9. An explanation via parallel mutation in mimic and model is excluded because the similarity is only superficial, e.g., different chemistry of pigments.

DISCUSSION AND CRITIQUE

Fisher attributed considerable general importance to his analysis of mimicry, as the following quotation (1930b, p. 147), as well as the printing of two colored plates, shows: "It will be clearly understood, from the argument of chapter one, that in the opinion of the author the bearings of genetical discoveries and in particular of the scheme of Mendelian inheritance upon evolutionary theory, is quite other than, and indeed opposite to, that which the pioneers of Mendelism originally took it to be. These were already, at the time of the rediscovery of Mendel's work, in the full current of that movement of evolutionary thought, which in the nineties of the last century has set in in favor of discontinuous origin for specific forms. It was natural enough therefore that the discontinuous elements in Mendelism should, without sufficiently critical scrutiny, have been interpreted as affording decisive evidence in favor of this view. *Nowhere perhaps in biology has this current of opinion introduced such serious discrepancies as in the interpretation of mimetic resemblance.* (Italics added.)" It is surprising that, in view of such evaluation, the problem has been discussed so little. Ford, a former student of Fisher, and Huxley, also Ford's former teacher, have accepted wholeheartedly Fisher's interpretation, as has also Carpenter. The present author, who had accepted Punnett's viewpoint formerly (1920, 1927) still clung to it in a recent book (1940); also Shull (1936) followed Punnett in his text on evolution. It has already been mentioned that such modern texts as Dobzhansky's and Mayr's do not even mention the problem.

A rather extensive discussion, not only of polymorphic mimetism, but of the entire subject has been presented by Nicholson (1927). He also accepts Punnett's views for such cases as the Papilios but demands slow selection of mutations for types of mimicry like similarity between beetles and ants. In the former cases he is ready to accept Punnett's views because the pattern systems of different families of butterflies are basically not different, and he proposes also a developmental explanation similar to one proposed by the present writer. We shall return to this point.

The most detailed recent discussion of the subject is found in Robson and Richards' book (1936). Their standpoint is more or less one of *non liquet.* Thus they state after presenting Punnett's and Fisher's views: "It may be noted that there is no *more* evidence for this theory (Fisher's) than there is for the simpler assumption (Punnett's)." They criticize especially the incompleteness of the factual data regarding variability, geographical distribution, ecology, and genetics, and emphasize the difficulties of the selectionist interpretation. They summarize their conclusions thus (p. 260): "The fact of mimicry, of striking resemblance between structurally unrelated forms, is well established, and the phenomenon is widespread, especially among insects. In a number of selected examples there is a considerable degree of probability that selection of warning patterns has brought about colour convergence. In another series of examples it is very difficult to see how selection could have led to the observed effects. In the majority of cases of mimetic resemblance, however, it is impossible at present to estimate to what extent, if at all, selection has been active. We are left, in fact, in a state of suspended judgment: it is probable that selection has played some part in the evolution of mimetic convergence, but it is normally impossible to say how large a part in any particular case." Later on they declare that it is certainly dangerous to use the mimicry theory as one of the main lines of support to the Natural Selection Theory. Another English geneticist, Watkins, has recently (1935) come out in favor of Punnett's viewpoint, without presenting a detailed discussion.

In view of the evolutionary importance of the problem I propose to inquire in detail into the entire body of relevant facts, omitting only the whole set of evidence in favor of mimicry itself, which I consider, with most biologists, an established interpretation.

A. Some general features

At the basis of all problems of adaptation, and especially of the origin of mimicry, lies the old question: how did the adaptation start? Darwin and Wallace (see above, p. 154) already realized the basic difficulty for slow evolution of mimicry, namely the first beginning. This must have had sufficient selective advantage to begin with, in order to be available for further natural selection. Darwin clearly believed that a small variation in the direction of the model did not suffice to start the ball rolling and therefore devised the idea that, at that time, the models were not very different from the mimic. This idea did not find much favor later and hardly solved the problem. Therefore, Punnett insisted that the similarity must have arisen in one step to be effective, and neither he nor Nicholson nor the present author found any difficulties in imagining such an event. On the other side, Fisher (1930b), as well as Ford, considered this impossible: "... while on the contrary the assumption of discontinuity becomes a burden upon the theory, involving as it does the definite improbability of hitting off a good resemblance at one shot" (p. 163). In another place (p. 165) Fisher adds that the origin of resemblance by a single mutation requires "the gratuitous assumption" that no change has occurred since the first mutation originated. I think that this statement amounts to begging the question; why should a successful, i.e., well adapted mutation not remain stable if conditions remain the same? Ford (1927) even asserts that "the numerous instances of this kind make it impossible to believe that selection has had to wait upon the fortuitous occurrence in each of a mutation having the varied effects required. This would be an almost impossible conclusion even if a single species only had been involved." To this we might remark that the "fortuitous occurrence" has as much chance to happen as the initial mutation required by the neo-Darwinian theory provided that the proper developmental system is present. We shall develop this point below.

It is certainly of no use to discuss such statements of belief or disbelief made by both sides to the discussion, and we shall therefore have to look for more objective criteria. But a few remarks on the general attitude to be assumed toward the problem as a whole may not be out of place. Let us assume that we should find in nature a species of flies with two forms, one normal and one wingless; or one normal and one with four wings; or, one normal and one with four halteres; and further that genetic analysis shows that the two types are inherited as simple Mendelian differences. The neo-Darwinian would conclude that the origin of such huge departures (actually on a level of macroevolutionary differences) could only be explained by gradual selection and accumulation of small modifiers. But actually these types are known to have arisen in the laboratory as single mutants in *Drosophila*. I should think that this example contains a warning to those who argue on the basis of a priori impossibilities. I cannot help feeling that in the case of mimicry the difficulty of the Neo-Darwinians to imagine an origin in a single step is based upon their a priori conviction that all cases of evolution *must* be explained by the selection of small deviations. Nobody, certainly, doubts that Fisher's theory of evolution of dominance by selection of modifiers is unassailable in principle. But this does not mean that every adaptation must be explained on the same basis. In passing judgment whether a definite type of evolution can be considered as possible or not we cannot trust our a priori disposition but must ask ourselves, as already stated, *whether the genetical and developmental system present in the forms under discussion permits or does not permit such a thing as evolution in one step.* We shall try to do this below.

There still remains, while discussing generalities, the problem of the first step as required by the neo-Darwinian explanation. The neo-Darwinian theory cannot work either before a resemblance of the mimic to the model is established which is at least so close that the predators are deceived, even if the similarity is not yet perfect. Thus everything is centered upon this initial step, which, if I understand it correctly, is assumed by Fisher and Ford to be due to a small mutation in the alleles *A* and *B* which we know to be the differentials that switch the pattern from non-mimic to mimic, in Fisher's language. This point seems to be generally passed over without much discussion. Fisher says that there is no reason to believe that, e.g., the *AAbb* form of *P. polytes* originally resembled much the present form *romulus* or was an "effective mimic" of *P. hector*. Ford speaks more concretely of any mutation which chances to give a "remote resemblance" to a more protected species, from which some advantage, however slight, might accrue. We must ask how remote the resemblance can be to have selective value. Can we really assume that the birds and monkeys and also mantids are such wonderful observers (or that some very clever ones among them are) to notice a "remote" resemblance and to be repelled by it? I think that this is asking too much. The minimum any selection theory of mimicry needs is a *fair* resemblance. But if we look at the actual specimens we realize that a fair resemblance would be not very much different from the present mimetic pattern. Therefore I cannot see why a mutant producing a fair resemblance cannot just as well produce a good resemblance.

There is another important point which is passed over in discussions. There exist cases in which both sexes are mimics. This shows that here the male also profits from mimetic advantage. In the majority of cases, however, the males are non-mimetic. Did they not need protection which is only needed by the egg-laying female? Why, then, are some males mimetic? Or does the mechanism of sex-controlled inheritance prevent the modifiers from acting in the male? If so, why have not male sex-controlled modifiers been selected if the male also needs protection? In some instances there are found non-mimetic and mimetic females. One should expect the non-mimetic females to disappear. In *P. memnon* there are two types of non-mimetic females and one mimetic. Polymorphism is thus present in the same species with and without mimicry, but the modifiers of two non-mimetic forms are not counter selected against. At least we should expect the non-mimetic females to have that remote resemblance. It would not be difficult to invent some kind of explanation for these occurrences, as has been done by statistical deliberations. But it is difficult to see why the simple explanation which does not require new hypotheses from case to case is rejected. If the second non-mimetic female is a mutant, why not the third mimetic one? But let us not continue with such general argumentation but analyze the factual basis as well as the logic of the opposing theories.

B. The model of sex

In presenting his theory of selection of modifiers for a switch reaction of a mutant allele, Fisher takes the determination of sex as an example to make his point clear. His followers have accepted this model, and Huxley (1943) has even improved on it by stating more clearly the supposed parallelism. The idea is that in the case of mimicry recombinations of pre-existing modifiers as well as new mutations (modifiers) are selected, all of which depend for their expression on the presence of the original mutant which started the mimetic resemblance. Thus the original gene-difference acts as a switch controlling the action of numerous other genes "precisely as occurs in the case of the primary sex-difference in regard to genetically sex-limited characters" (p. 102). This sounds convincing at its face value, but the comparison cannot stand a closer scrutiny of the details. Let us first realize what we are asked to accept as the probable course of evolution of mimetic resemblance, for which the assumption of a similar situation in the evolution of sex is used as an illustration. There must have been present at the time of the first mutation of the "switch-gene" towards the "remote mimetic resemblance" a series of modifiers capable of changing the effect of that mutant, and some of the modifiers or some combinations of these were acting in a direction which, by chance, improved the mimetic resemblance. This involves the assumption that modifiers for all kinds of changes are always available for selection, therefore also those which by pure chance change the pattern towards that of the model. I note that this situation is not regarded as improbable, while a single "fortuitous" mutant (see quotation above on p. 157) is considered as highly improbable. These modifiers were slowly selected by the clever birds, monkeys, and mantids who could distinguish the small improvements towards the unpalatable model. Simultaneously other mutants appeared and were selected if they had the property of acting only in the presence of the switch-gene and, in addition, acted in the direction of further improving the mimetic pattern. (This requires, of course, that all other mutants could not compete.) In a case like *P. dardanus* or *polytes* a second switch-mutant (at least) appeared, and this whole process was simultaneously carried out for the second mimetic pattern. In addition, the two mutants must have acquired the dominance relations required by the genetic facts, which in themselves are assumed to be the products of selection of dominance modifiers. Further, the nature of the mutants and their consequent effects upon the phenotype must have been such as is required by the known interaction of two different dominants in producing only the three types of females in the different possible recombinations (see Table 3). Finally, in most cases, the mechanism of sex-controlled heredity was present from the beginning or established later, and *all* the selected groups of modifiers belonged to the group of sex-controlled mutants.

This is the type of evolution which is compared with the evolution of sex. The switch-gene is compared to the primary sex-genes. We could point out that the switch action of the primary sex determinants, whether one or many, is made possible by a unique chromosomal mechanism which controls a balance situation in two possible directions. No similar mechanism is known outside of sex-determination. But let us forget this difficulty and accept the rather superficial comparison of the two switch-processes as permissible. In the case of mimicry the "switch-gene" is a wing-pattern mutant towards the pattern of the model. The supposed modifiers and secondary mutants also affect the pattern in the same direction, in presence of the "switch-gene." In sex, the "switch-gene" affects the development of the sex-cells and their surroundings (gonads, maybe ducts). A parallel to the mimicry case would require that modifiers and mutants are selected which act upon sex-cells and gonads. But what is meant in the comparison is a selection of somatic characters which have nothing to do with sex though they are brought under sex-control in some cases. Let us assume that horns in sheep or antlers in deer had been selected in the neo-Darwinian way. The same may be true for the differences in skeleton, muscles, brain, size, shape, etc., of the two sexes. This means, if it actually happened that way, that a series of simultaneous or consecutive changes were produced by selection of mutants and modifiers each of which improved upon some different system of the body, but none of them upon the pattern (sex) controlled by the "switch-gene." A parallelism between the two processes under comparison could be established only if, in the sphere of sex, selection during evolution produced different types of primary sexes, which is more or less absurd, at least in higher animals. Thus the comparison with evolution of secondary sex-characters is completely misleading and does not furnish a model for the supposed type of evolution of mimicry. Actually the only *tertium comparationis* is the fact of sex-control itself, which in general means the subjection of somatic characters to a switch-reaction with the products of the primary sex-determiners or of their secondary products, the sex hormones. But the problem of sex control is not at all under discussion, especially as sex-controlled inheritance is not necessarily connected with mimicry.

At this point it will be objected that mimicry actually affects many different characters, not only the pattern. In the Papilios the tails might be included and the type of flight, in others some other characters. This subject will be considered below. Here it suffices to say that the decisive part of the mimicry under consideration is the wing pattern. Otherwise one could not speak, as has been done, of tailed mimics when the model has no tails (see fig. 2d, e). Nobody who accepts Punnett's theory would deny the possibility of mutations in other organs and their selection, which might perfect still more the similarity already produced by the wing pattern. But the real problem remains the wing pattern which alone covers the major part, actually all or almost all, of the adaptation under discussion.

(*To be concluded*)

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

DARWIN AND SOCIAL THEORY IN AMERICA

A review of *Social Darwinism in American Thought 1860-1915*, by Richard Hofstadter. *Philadelphia* (The American Historical Association; University of Pennsylvania Press); *London*, (Oxford University Press). $2.50. viii + 191 pp. 1944.

By Raymond P. Hawes, Goucher College.

In this engagingly written book Hofstadter is concerned with the coming of evolutionary ideas to America, the impact of these ideas on American thought and life and the reactions of outstanding Americans to them—including attempts on the part of American thinkers to reinterpret them or to replace them. The author's main interest is in the implications of biological concepts for ethics and social action.

Instrumental in introducing Darwin and Spencer to American readers were chiefly Asa Gray, E L. Youmans, John Fiske and Chauncey Wright. William James started the stream-lining of psychology and philosophy along evolutionary lines, and William Graham Sumner did the same for the social sciences. In the sixties and early seventies, biologists—notably O. C. Marsh—contributed to the evidences of evolution. By 1873 it was possible for an editor to refer to the "'universal drenching' of belles lettres and journalism with natural selection." In the eighties "evolution" found its way into the churches, and opposition to it on the part of the outstanding Protestant theologians died out.

The ideas of Darwin and Spencer exerted a tremendous influence on American thought, and the uses to which these ideas were put were exceedingly varied. Many saw in them a support for a laissez faire economics and politics. Indeed, Spencer himself (followed in part by Sumner) outdid the originators of the laissez faire philosophy when he opposed state-financed education, health measures, and relief for the poor. The principle of natural selection was thought to imply that the unfit should perish and that among the unfit should be counted—along with the physically and mentally defective and those given to vice—the poor. Spencer was far from being alone in holding that it is a mistake to interfere with natural laws and with the natural, gradual growth of society, even by means of the mildest social legislation; while to attempt seriously to remodel the whole social system is "the greatest folly of which a man can be capable" (Sumner).

It was easy to reason that social evolution, like biological evolution, involves both a struggle of life against its non-living environment and a struggle of organism against organism and group against group. From this it seemed to follow that unrestricted economic competition is an essential of social progress; that those who scale the heights of power and wealth are necessarily the fittest; that these "superior" persons deserve whatever they can get and merit the utmost acclaim of their fellows; and that the losers should accept any hardship involved as a necessity imposed by nature. In short, the control of economic change by automatic adjustments in accordance with natural laws appeared to be the sole basis for freedom, justice, prosperity, and progress. To many it also seemed to follow that (despite Spencer's dream of the ultimate triumph of altruism and pacificism) war is an inescapable element of human life—quite clearly if society is founded on the man:land ratio. In the minds of a few, war took on the guise of a boon to mankind as an indispensable method of social evolution.

From these conclusions—perhaps in some cases with the help of Spencer's organismic conception of society and De Vries's mutation theory, which, as against Spencer's gradualism, seemed to legitimize sudden change—it was no great step to the acceptance of the validity of inferences such as the following. Economic misery and the irresponsibility of the rich are goods, not evils. The masses should follow "leaders" selected for them by "natural" processes. Brutal self-assertion and tyranny are justified. Imperialistic expansion (or conquest) is a nation's manifest destiny. Weaker (or backward) peoples and weaker (or "inferior") races should be subjugated (or eliminated) by the stronger (or "superior"). The Aryan (or the Teuton or the Anglo-Saxon or the English-speaking people) is superior. Security lies in outstripping all other groups in military and industrial, if not also in population, "preparedness." The most important aspect of education is the cultivation of personal prowess and the martial virtues. Group suicide and group degeneracy are the greatest sins. Eugenics is the panacea.

In point of fact, those were not wanting who leaped to the most sweeping generalizations: that might always makes right; that human life as such merits no respect; that altruism, humanitarianism, and Christian ethics are bad, and that atheism is preferable to religion. According to Sumner, not only are there no natural rights, but also no ethical standards whatsoever—apart from "folkways."

Ideas such as the foregoing carried Social Darwinism a long way from Darwin, as Hofstadter clearly recognizes. While Darwin's *Origin of Species* was "Hobbesian in spirit," he finds, and while Darwin's remarks on "Natural Selection as Affecting Civilized Nations" in his *Descent of Man* were Spencerian and Malthusian in part, nevertheless, Darwin counseled against a ruthless elimination of the weak, however injurious to the race might be the perpetuation of our practice of caring for the weak and allowing them to propagate. Far from holding that might is right, Darwin discovered natural roots for sympathy and cooperation; asserted that man's moral sense is a critical factor in group survival; and thought of the "fittest" as those best adapted to existing conditions. The latter were not necessarily the strongest, far less the most brutal. As Nasmyth (following Kropotkin) discerned, in Darwin's view man owes his dominant position in the universe not so much to the struggle of individual against individual or to contentiousness, as to his struggle against his environment, along with unselfishness, mutual aid, and social coherence. Patten (followed by Cooley) called attention to Darwin's assumption that man is plastic or pliable with reference to his environment, so that circumstances may determine his characteristics. According to David Starr Jordan, Darwin believed that war is dysgenic. At the very inception of the evolutionary hypothesis in America, Asa Gray had tried to show that Darwin was "explicitly theistic"; while, at the turn of the century, Dewey suggested that if Darwin's "existing conditions" may be interpreted to include "the existing social structure with all the habits, demands and ideals which are found in it," we need not "go outside nature to find a warrant for the ethical process." Hofstadter might have pointed out that today outstanding biologists are developing this Darwinian interpretation of the application of biological ideas to ethics and social action rather than the "Social Darwinism" outlined above.

Hofstadter thinks that a new trend in American thought appears with the work of Lester Ward—a trend which was developed by a number of sociologists, economists, and philosophers, and one which in the end came to prevail over what had been known as Social Darwinism. Social evolution now comes to be considered a unique level of organization, with novelties "which are not predictable from a knowledge of their antecedents." On this social level of evolution we find new natural laws and a new principle of selection—variously called social, mental, purposive, artificial, and rational. Malthus's law has no validity for man, and the other laws which control the animal world apply to man in a very limited sense only. Not overpopulation and the niggardliness of nature, but the injustice of society becomes the villain in the piece, because with ever more rapid technological progress each new person can produce more than the last. Economics should be based on "abundance," not "want." On the social level at least, natural laws are not fixed and do not exclude reform. While the environment transforms the animal, man transforms the environment; control replaces mere adjustment.

Life on the animal level is no longer regarded—in Spencerian fashion—as a mere correspondence (or equilibrium) of two sets of relationships nor—in Darwinian fashion—as a mere struggle for existence. As William James put it, when consciousness appears upon the scene, the struggle is for "ends" (e.g., enjoyments); on the human level we are "fighters for the better." Neither animal struggle nor human competition selects the fittest in the sense of the best. A circle is involved in defining the fit as those that survive and then explaining their survival in terms of their "fitness." War and intraspecific competition are wasteful and injurious to the species and economic rivalry is self-defeating in that it generates competition-destroying monopolies. Natural laws no longer operate automatically to human advantage, and the favors of nature are not distributed according to merit. There is no biological or other "natural" basis for either laissez faire economics or for power politics.

In sharp contrast to natural selection, "rational selection" saves resources and produces superior beings. Man advances through the protection of the weak, through mutual aid and through responsible cooperation. From now on progress will come only by the exercise of free effort, through a deliberate selection between real possibilities, by intelligent planning on a social scale, and by using one part of the environment to reconstruct another. So far as government is democratic and aims at the good of all, the state should interfere with the automatic processes of nature. The functions of the state should be determined experimentally, but with the proviso that "human" values rather than impersonal values be kept in mind as the goal. In the words with which Hofstadter characterizes this new attitude: "Man's task is not to imitate the laws of nature, but to observe them, appropriate them, direct them."

This point of view pins its faith on non-eugenic means of progress, primarily: improving the environment, opening up opportunities and, above all, education. Ward, like Spencer—following Lamarck rather than Weismann—anticipated gains from "use-inheritance" in addition to the usual values of education. It also came to be widely believed that sociology should be based more on psychology than on biology, though Ward was quick to add that all sociologists should also be biologists. Pragmatists showed that the older psychologies (including Ward's own) were inappropriate as a basis for the social sciences, and promptly supplied a new psychology which was at once more "biological" and more "social" than the old. More specifically, mind must be considered: (1) a participant in progress, experimentally reconstructing both its environment and itself—not a mere spectator of inevitable change; (2) a "structure of propensities, interests and habits"—rather than a "mere machine for the reception and registration of pleasure and pain stimuli"; (3) largely a social product, and also socially oriented when operating on its highest (ethical) plane. For such a mind ideas become plans of action and instruments of control.

Hofstadter concludes that Darwinism "was a neutral instrument capable of supporting opposite ideologies." The earlier version of Social Darwinism was ruggedly individualistic because it came to birth in an age of unrestrained economic competition and unprincipled politics. In proportion as this "dream of personal conquest" met frustration, Darwinian collectivism of the nationalist and racist types pushed to the front and continued through an age of group assertiveness and competition down to the first World War, when Anglo-Saxon peoples "discovered" that Darwinian militarism was precisely what they were fighting. "As long as there is a strong element of predacity in society," Social Darwinism may rise again. At present, however, "most humanists," in attempting to understand society: (1) reject such ideas as "survival of the fittest"; (2) assume the uniqueness of the social level of evolution; (3) agree that progress rests on advances in technology and in social organization rather than on breeding and selective elimination; and (4) contend that naturalism as a philosophy does not preclude "moral sanctions which can be employed for the common good."

Hofstadter's book is well documented and his citations from source material are aptly chosen. It is possible that some readers would have welcomed a more extended discussion of the treatment of biological concepts by non-pragmatic writers. It must be admitted that it is hard to pick a quarrel with the author's conclusions. Very probably, most humanists among biologists—unlike those to whom Hofstadter alludes when he writes of "most humanists"—would not reject such ideas as "the survival of the fittest" in attempting to understand society. Doubtless one may be permitted to raise an eyebrow at an occasional assertion or implication, such as. (1) the statement that Herbert Spencer's philosophy is "a product of English industrialism"; (2) the attribution of some of Lester Ward's characteristic beliefs to his "humble origins"; or (3) the seeming implication (probably unintended) of certain passages in the author's "Conclusion" that the generally accepted economic (or political) system of an age determines how scientific discoveries are philosophically interpreted. But these matters are merely minor overtones in an excellent piece of work which constitutes a valuable supplement to the efforts of Beard, Gabriel, and Curti to interpret America's past.

REVIEWS AND BRIEF NOTICES

GENERAL BIOLOGY

THE BOOK OF NATURALISTS: *An Anthology of the Best Natural History.*

By William Beebe. Alfred A. Knopf, New York. $3.50. xiv + 499 pp.; 3 plates. 1944.

It took courage and must have given keen pleasure to collect in one volume "the best" from the great writings in the vast field of natural history. In his preface the author mentions "an invitation to every reader to damn my selection." Beebe's selection has evidently been influenced as much by the perfection of style and the inspired art of composition as by the scientific value and originality of the great contributions to natural history. Unquestionably he has succeeded in making a uniformly stimulating, charming, and thoroughly readable book.

With selections from the writings of forty-six authors, arranged chronologically, this anthology reflects the development of natural history from Aristotle to the present day. As a matter of fact, the author sees the inception of recorded natural history in the cave paintings from the stone age and opens the collected essays with three pictures of such admirable paintings by "An unknown Magdalenian (Circa 25,000–20,000 B.C.)." The first part of the book depicts the slow growth of man's understanding of animals and plants from early Greek times through the Middle Ages and beyond the Renaissance. It quotes from the writings of Pliny the Elder, Theobaldus, Gesner, Leeuwenhoek, Linnaeus, Humboldt, Thoreau, and others. The much larger, second part begins with Darwin and Wallace, includes Agassiz, Belt, Maeterlinck, Burroughs, and many more, and ranges to such contemporaries as Chapman, Julian Huxley, Seton, and Stefansson. The majority of the 31 selections for the second part have been chosen chiefly for their value as *literary natural his-*

tory and for having claim to consideration on the basis of "beauty of form or emotional effect."

Regarding subject matter, plants fare rather poorly, but animals are well represented by sample writings for nearly every interest from protozoa to mollusks, arthropods, and all the main groups of vertebrates. Besides which, there are essays on evolution, protective coloration, bird migration, the aims, adventures, and tribulations of naturalists, and other topics. Geographically the subjects range around the globe and from the Arctic to the Antarctic as well as from the Himalayas to under water. Eleven different nationalities are represented among the authors.

Unfortunately, modesty forbade the inclusion of selections from Beebe's own fascinating descriptions and interpretations of nature. However, the author's introductions to the two parts of his book make up in part for the deficiency, as they form interesting essays, equal in quality to the selected writings by others. Also noteworthy are Beebe's brief biographical notes concerning the authors selected for this anthology.

ADOLPH H. SCHULTZ

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SIERRAN CABIN . . . FROM SKYSCRAPER. *A Tale of the Sierran Piedmont.*

By C. M. Goethe. The Keystone Press, Sacramento and San Francisco. $1.25. xiii + 185 pp. 1943.

This unusual book mingles natural history and plant ecology, Californian folklore, and propaganda for eugenics. Its style is highly individual, liberally besprinkled with capitals, literary and non-literary allusions, and odd bits of verse. The illustrations are abundant and excellent, but foreign words and scientific names are frequently mis-spelled.

It is difficult to determine whether the Main theme is that of the Mental and Spiritual REGENERATION of Skyscraper Man through the observation of Nature, or whether it is the DYSGENIC character of American Life and the Necessity for increasing the Reproductive rate of the Intelligent. Perhaps the balance favors the latter. The argument for positive Eugenics by controlling DIFFERENTIAL BIRTH-RATES is based on observations of Adaptation, Survival, and Extinction among members of the Californian Flora. But the author does not trouble to consider the difference between such interspecific comparisons and the intraspecific competition of human types, and blandly assumes that the genetic bases of mental differences and social behavior in man are comparable to those between Araucarian and yellow pines, for example. The importance of environmental factors in modifying mental differences and social behavior is simply ignored.

There is, nonetheless, much that is interesting for casual perusal between these covers.

BENTLEY GLASS

MAN DOES NOT STAND ALONE.

By A. Cressy Morrison. Fleming H. Revell Company, New York, London and Edinburgh. $1.25. 107 pp. 1944.

The title of this book was chosen as a challenge to Julian Huxley's concepts, recently developed in *Man Stands Alone*. Morrison, a chemist and former member of the National Research Council, approaches the problem of life from the standpoint of an avowed deist. He has undertaken to write a modern Bridgewater treatise, with arguments from the "fitness of the environment" and the marvels of adaptation. He accepts some sort of evolution, but has perhaps never heard of natural selection (at least it appears not to be mentioned anywhere). The following line of reasoning is fairly typical: "As the number of eyes in animals ranges from two to thousands, and all are different, Nature [sic] would have had a big job in developing the science of optics unless somewhere along the line there was a little help from Intelligence."

This edifice of biological logic is, however, completely vitiated by being based on the most astonishing statistical fallacy. The main thesis of the author, with which he begins and with which he closes his discussion, is simply that the existing universe could not have arisen by chance, because the mathematical probability of such an infinite number of coincidences is infinitesimal. He illustrates· the chance of picking at random a single white marble from a bag containing 100 marbles, the other 99 black, is 1/100; of doing it twice in succession in 1/100 × 1/100; etc., so that the probability of doing it five or more times in succession is altogether improbable.

Quite so! But let us suppose that each marble in the one hundred is identifiable, say by number. Then *any* sequence of five is equally improbable. Yet if you draw a sequence of five, regardless of what it is, you make an actuality of a coincidence that is highly improbable, as far as predictability is concerned. Every baby that is born represents a combination of paternal and maternal genes that is, from the standpoint of prediction, only one of trillions of possibilities. Yet babies somehow continue to be born! Of course, this, too, might be due to the machinations of Intelligence, the same Intelligence who determines how the penny will fall. Perhaps the author does not realize that he has reasoned himself into a position from which it follows that his God and Chance are one.

BENTLEY GLASS

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THE NATURALIST'S LEXICON. *A List of Classical Greek and Latin Words Used or Suitable for Use in Biological Nomenclature, with Abridged English-Classical Supplement.*

By Robert S. Woods. Abbey Garden Press, Pasadena. $2.75. xviii + 282 pp. 1944.

The preface to this little lexicon opens with the claim: "Since Greek and Latin are seldom included in the studies of those who specialize in any branch of biology, scientific names are to most students of natural history simply meaningless and easily forgotten combinations of letters . . . " Even the many adequately educated biologists will welcome this convenient and well printed dictionary, regarding which the author states: "It is the purpose of this work to try to render more available to naturalists the definitions and correct pronunciations of these names which they so constantly encounter . . . . The intention has been to include not only classical words which have actually been employed in the construction of scientific names of animals and plants, but all others which might seem applicable to that purpose."

The "Classical-English" section contains 257 pages, listing alphabetically Greek and Latin words used in taxonomy and their equivalents in English. A philologist, rather than a biologist, may be able to explain the curious fact that words beginning with the letters *a*, *c*, *p*, and *s* seem to be far more common in taxonomy than words starting with other letters. At least this lexicon devotes a total of 125 pages to the four former letters (38 pages to the letter *c* alone), whereas only a total of 132 pages to all remaining letters. The "English-Classical" section of only 22 pages is too condensed to be of real service. For instance, only 66 names of mammals are listed and only 101 parts of the body, the latter under the inappropriate heading "Physiology."

This thin volume contains nothing that is not to be found also in the larger, general Greek and Latin dictionaries. To private libraries of biologists *The Naturalist's Lexicon* will form a handy addition

ADOLPH H SCHULTZ

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EXPLORING BIOLOGY. *New Edition.*

By Ella Thea Smith. Harcourt, Brace and Company, New York. $2.24; tests, 36 cents. xxii + 619 pp. 1943.

EXPLORING BIOLOGY WORK BOOK.

By Ella Thea Smith and Lynda M. Weber. Harcourt, Brace and Company, New York. $1.00 (paper). vi + 154 pp.; tests, 16 pp. 1944.

The organization of this high school text is that known as the Unit-Problem. There are eight units, subdivided into thirty-one problems. Each unit deals with a basic understanding. These include the kinds of animals and plants and man's place among them, metabolism, health and disease, the interdependence of life, the bases of behavior, reproduction and development, heredity, and evolution. Each unit begins with a dramatic episode intended to serve as the first step in motivation. A number of these are exceedingly well written. Each of the problems is then introduced with a question, discussed accurately and with great clarity, involving a minimum use of technical terms, and concluded with directions for individual and group study in laboratory and in the out-of-doors, with a test of the factual information and the generalizations covered, thought problems, references, extra reading for ambitious students, and a list of the minimum number of new terms considered indispensable additions to the vocabulary. Each unit ends with a general summary.

The text is in two columns, a feature some will like and others dislike. The abundant half-tone illustrations are well chosen but have suffered from mediocre printing and paper. The diagrams are exceptionally good. There is a section of suggestions for the classroom library, a full and accurate glossary, and a very full index. An envelope containing a series of 29 tests of the objective type, prepared with great technical care, is also included.

The workbook to accompany the text has been prepared with the same thorough care and evident skill that went into the text. Seventy-seven exercises are included, and space for drawings, records, and answers to questions is provided The sheets are punched and removable There is a supplementary pamphlet of tests supplied to the teacher for each student.

There are too many excellent features of this textbook for individual consideration. After having examined and reviewed a considerable number of other high school texts, many of them good, the reviewer is more than ever impressed by the present one. In no other has he seen the standard of factual accuracy so high, the clarity of presentation so continuous, the provision of helps for teacher and students so abundant. Motivation and organization have been carefully thought out. The preview is one of the best introductions to biology to be found. The view of the entire subject is comprehensive and well balanced, plant, animal, and human biology being closely interknit. The style is appropriate for high school students.

No one but a high school teacher of a most exceptional character could have written this book. Other high school teachers should give it an enthusiastic reception.

BENTLEY GLASS

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A FIELD COLLECTOR'S MANUAL IN NATURAL HISTORY. (*Publication 3766*).

Prepared by Members of the Staff of the Smithsonian Institution. The Smithsonian Institution, Washington. 50 cents (paper). iv + 118 pp. 1944.

In this pocket manual there are clear and concise directions for collecting, killing, preserving, packing and shipping most kinds of animals and plants. Prepared especially for men of the armed services abroad, it also contains some information on occurrence and dangerous forms. There is also a brief section on anthropological materials; a considerable one on fossils; and, finally, one on other types of geological specimens. It is to be hoped that this handbook will serve as a stimulus to our men, who have so unparalleled an opportunity to enrich American museum collections. What they need to know, in so far as a manual can give it, is here. Experience will supply the rest.

* * *

BIBLIOGRAPHY OF REFERENCES TO THE LITERATURE ON THE MINOR ELEMENTS *and Their Relation to Plant and Animal Nutrition. Fifth Supplement to the Third Edition.*

Compiled by L. G. Willis. Chilean Nitrate Educational Bureau, Inc., New York. Paper. 96 pp. 1944.

This supplement abstracts additional literature on the role in nutrition of Al, Sb, As, Ba, B, Br, Cd, Ca, Cl, Cr, Co, Cu, F, Ga, Ge, I, Fe, Pb, Li, Mg, Mn, Hg, Mb, N, Pt, Ra, Rb, Se, Si, Ag, Na, Sr, S, Tl, Th, Sn, Ti, U, V, Zn, Zr, and the rare earths. There are four indexes, respectively of elements, of plants, of animals, and of authors. To all workers in the fields of nutrition this bulletin should be indispensable, and to many others it will be of great value.

ECOLOGY

TRANSACTIONS OF THE NINTH NORTH AMERICAN WILDLIFE CONFERENCE *April 24, 25 and 26, 1944, Chicago, Illinois.*

Edited by Ethel M. Quee. American Wildlife Institute, Washington. $1.00 (paper). iii + 376 pp. 1944.

A good idea of the progress and changing ideas in the field of wildlife management can be obtained by reading through these transactions. One is impressed by the number of articles concerned with controlling the larger game that have increased to or beyond the optimum carrying-capacities of the areas established for their propagation, especially the winter ranges. Such seems to be the case for mule deer in Utah and Oregon, and for elk in Jackson Hole.

Again, emphasis is placed not so much on the direct control of the stock as on the management of the habitat. In fact, wildlife management has so changed its methods in the past few years that many of the hunting and fishing laws are now antiquated, and reforms are needed. One startling idea proposed is the abandonment of all fresh-water fishing regulations,—this by Langlois, who believes that regulation of fishermen is negative, expensive and futile. Habitat improvement is a positive procedure and a justifiable way of spending the fishing-license funds. Another observation that may surprise some, though certainly not the ecologist, is the discovery by Cartwright that the Hungarian partridge and the sharp-tailed grouse have been saved from practical decimation by predators. The destruction of a substantial portion of first and second nestings by the predators was found to stagger the nesting attempts, thus becoming a major factor in the survival of the species during periods of inclement weather. This is certainly a far cry from the formerly all too common (and still very much in existence) policies of "shoot the vermin," often wantonly approved by conservationists themselves.

The deep sea fisheries are included for the first time in the conference program, and several articles discuss not only the problems and methods of marine fish management, but also some of the legal aspects of maritime fishing, with suggestions for post-war changes.

Two interesting reports discuss the effects of soil fertility and the relation of soil types to the abundance and quality of wildlife. Other papers deal with the role of government and private organizations in their efforts to cooperate with the Fish and Wildlife Service and state conservation agencies in protecting and managing the lands and waters for wildlife. Several speakers sharply attacked certain federal agencies for their utter disregard of wildlife; the justification for these castigations may be complete or partial, but at least their airing indicates that the program was well represented by all interests. The Transactions close with an important section devoted to the place of conservation in the educational programs of our schools and colleges.

HENRI SEIBERT

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A PRELIMINARY STUDY OF THE THERMAL REQUIREMENTS OF DESERT REPTILES. *Bulletin of the American Museum of Natural History, Volume 83: Article 5.*

By Raymond Bridgman Cowles and Charles Mitchill Bogert. American Museum of Natural History, New York. (paper). Pp. 261-296; plates 19-29. 1944.

This paper presents the interesting results of a careful study of the thermal relations of desert lizards and snakes. The data are carefully selected for freedom from the influence of extraneous factors and consequently are not extensive. The conclusions will be of interest not only to ecologists but also to students of animal behavior and in particular of evolution. The mean temperatures of the normal activity range and the critical maxima are considerably lower than those reported in some earlier investigations, or than might have been expected in desert poikilotherms.

EVOLUTION

EVOLUTIONARY ETHICS. *The Romanes Lecture Delivered in the Sheldonian Theatre 11 June 1943.*

By Julian Huxley. Oxford University Press, London. 75 cents (paper). 84 pp. 1943.

A little over fifty years ago T. H. Huxley, valiant pioneer of the theory of evolution, gave the Romanes lecture on "Evolution and Ethics." In 1943 his grandson, Julian Huxley, one of the foremost modern students of evolution, delivered the Romanes lecture on the same subject. It is reprinted in this pamphlet. The approach of the two biologists to a relation between ethics and evolution is yet basically different. For the elder Huxley, values were founded on immutable, self-evident principles, and ethical progress consisted rather in "combating" the cosmic evolutionary process than in forming part of it. For Julian Huxley, there are no absolute values. He sees evolutionary processes not only on the inorganic and biological level, but equally on the sociological level. By thus extending the concept of evolution he finds an escape from ethical relativism. The trend of evolution yields criteria to judge moral values and discriminate between more advanced and more primitive forms.

Before discussing the contribution of the concept of evolution to ethics, the development of ethical behavior from early childhood to maturity is described, though in a rather superficial and dogmatic fashion. The deciding influence of the environment on the formation of the ethical values is stressed. Thus we find an enormous variety of ethical systems, but in the seeming chaos an evolutionary trend can be discovered. It is this trend which Huxley thinks will save us from ethical relativism and give us the right to decide that one system is more right than another.

What are these principles of evolutionary ethics? Characteristic of evolution are increase in complexity and degree of organization. In the ethical field this means that good is what helps the fullest development of the human individuality, the progressive realization of possibilities which have value for their own sake. Social organization is a means for the advance of the individual; it is good when it serves that development of individuals. Social change is to be encouraged because it leads to a realization of ever more possibilities in evolution. Yet this change can only be realistic and effective if it is based on knowledge: thus science receives increased moral value.

The main points which crystallize out of the discussion are: 1. There is a manifoldness of ethical values in various human groups. The ethical behavior of the individual develops under the formative influence of the specific cultural environment. 2. There is not only variation but evolution. We can apply the principles of evolution to the social level. As a matter of fact evolution is taking place at present at the fastest rate on the level of social, cultural organization. Ethical values are not equally right. The characteristic trends in the evolutionary process give us criteria to judge different ethical systems. But no new ethics is developed here. The content of this "Evolutionary Ethics" is not new. In fact, Huxley's ethics is essentially the ethics of the humanistic-Christian individualist, and it retains all the conflicts and contradictions which have led into the moral chaos of the present Western Civilization. We also find little new insight into the puzzles of ethical behavior or the characteristics of its development in the individual, or its evolution in society. Nevertheless, these lectures are of interest as an attempt to expand evolutionary concepts to a sociological field like ethics and as the expression of the point of view of an eminent modern biologist on one of the most important problems of our society.

HANS RIS

GENETICS AND CYTOLOGY

ELEMENTS OF BACTERIAL CYTOLOGY.

By Georges Knaysi. Comstock Publishing Company, Ithaca. $3.50. xii + 209 pp. 1944.

The purpose of this book is to give a brief and interpretative presentation of bacterial cytology. No attempt is made to include all of the important literature, since, according to the author, this would defeat the purpose of the book. However, much original literature on a variety of subjects is covered. The topics presented in the thirteen chapters include: Form and Size of the Bacterial Cell; The Cytoplasm and the Nucleus; The Cell Wall and the Slime Layer; Physico-Chemical Properties of the Bacterial Membranes; Cell Division; Vacuoles and Reserve Material; The Motion of Bacteria; The Spores of Bacteria; Staining; Bacterial Cultures; Cytology of the Actinomycetes; Cytology of the Spirochetes; and Cytology of the Myxobacteria. The book is well illustrated with 91 figures, 10 plates and 18 tables

Because of the presentation of such a variety of topics in such brief form, most of the chapters serve only as outlines of the subject. The significance of a great deal of the material is inadequately discussed, and lack of additional data may, in many cases, leave the reader confused. For example: the author uses the term "bacterial nucleus" throughout the book but fails, in the chapter dealing with "The Cytoplasm and the Nucleus," to give the criteria or definitions which the cytologist uses for the bacterial nucleus. Some opinions to the contrary, the hypothesis that the bacteria have no nucleus does not deny the existence of a material capable of giving the usual staining reactions obtained with nuclei; nor does it deny the existence of a mechanism of inheritance. The continued use of the term "bacterial nucleus" throughout the book, is, therefore, misleading. In the chapter dealing with the "Physico-Chemical Properties of the Bacterial Membranes" one would like to know the evidence which leads the author to conclude that narcotics reduce the permeability of the cell membrane. In other forms, the few experiments which indicate a reduction in permeability of the cell membrane under narcosis are still open to question, while many experiments indicate an increase in permeability under narcosis. The experiments dealing with the bacterial cell membrane are even more inconclusive. The effect of pH on the passage of solutes through the cell membrane is not considered, although one might well expect such in relation to morphological changes during growth. There are a number of topics that one would like to have seen discussed in a book of this type. To some it may seem unfortunate that a chapter is not devoted to a consideration of bacterial cytology and taxonomy. The book will be found useful, however, by students of bacteriology as a guide to the field of bacterial cytology.

W. D. McElroy

GENERAL AND SYSTEMATIC BOTANY

Wild Flowers in Britain.
By Geoffrey Grigson. William Collins of London; Hastings House, New York. 4s. 6d; $1.25. 48 pp.; 12 plates. 1944.

This very artistic and rather charming little book is written, interestingly enough, by a poet who has acquired an unusually thorough knowledge of the flowers which grow wild in the British Isles. In his account of the wild flowers, common and uncommon to the English landscape at various seasons, he has included many curious and interesting facts about their history, distribution, and adaptability. The text is well illustrated with twelve full-page color plates and twenty-two illustrations in black and white, many of them full-page. All are engravings reproduced from 18th and 19th century manuscripts. The book is not a key.

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Dependent Plants. *The Basic Science Education Series.*
By Bertha Morris Parker, with the collaboration of Ruth M. Addoms. Row, Peterson and Company, Evanston, Illinois. 32 cents; 24 cents in quantities of 5 or more. Paper. 36 pp. 1944.

This booklet introduces to readers of these columns a series of science books for children in grade school that, to judge from the present example, deserves the widest attention and use. The quality of the illustrations, most of them in color, is of such excellence both in drawing and in printing that adult scientists may want to add it to their personal libraries. The text, dealing with mushrooms, molds, slime molds, yeasts, bacteria and heterophytic seed plants, is scientifically accurate, on the one hand, and, on the other, is told in a manner to appeal to a child in the intermediate school grades. It is hard to imagine one whose interest would fail to be quickened by the story, or who would not be tempted to try at least some of the experiments and observational activities listed at the end under the heading, "See For Yourself."

Travelers All, *The Story of How Plants Go Places.*
By Irma E. Webber. William R. Scott, Inc., New York. $1.25. 30 pp. 1944.

This book for young children tells in text and pictures of various ways by which plants achieve dispersal. The colored pictures will no doubt appeal to children, but they are crudely printed for a book so expensive. The text is well written, and children of eight to ten years to whom it was read gave every sign of interest and appreciation.

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Wild Flowers and Weeds.
By G. H. Copley. John Crowther, London. 8s 6d. 164 pp. No date.

This book will be of interest to a strictly limited public—the English country walkers who have just begun to look at and enquire into the nature of the trees, herbs, and flowers which help to make up "scenery." It might appeal especially to children as an introduction to plant life and natural history, but the reviewer is a little doubtful as to whether its chatty style will be palatable to many adults, and in any case a real nature enthusiast will quickly graduate to more advanced reference books. The last part of the book, dealing with weeds and their control, is, however, of real practical importance, and the reader who starts out with sheer curiosity about wild flowers will at least end up with a gobbet of sound instruction on weeds. It is unfortunate that the reproductions of wild flower photographs are technically very poor. The price seems exorbitant for a book of such slight content judging by pre-war standards, but presumably that is because books have become a luxury product in war-time Britain.

Eileen Sutton Gersh

GENERAL AND SYSTEMATIC ZOOLOGY

One Day on Beetle Rock.
By Sally Carrighar. Alfred A. Knopf, New York. $2.75. 196 pp. 1944.

This is the tale of one day, the same day, in the lives of the animals of Beetle Rock—the weasel and her kits, the unmated injured Sierran grouse, the lively chickaree who had to get a nest built, the black bear and her two cubs, the lizard who nearly lost his life and found a mate, the coyote family from the plains which found the new life in the mountains difficult, the deer mouse, the Steller jay, and the mule deer who was growing too old to reign unchallenged as herd buck. The interplay of the lives of these inhabitants of the Rock is traced through thunder storm and through danger, in the early warmth of spring and the coolness of mountain air, from the stillness before the dawn to the darkness of a new night. Only a keen observer and a true lover of mountains and forests and the living things that inhabit them could have written so unaffectedly of these simple doings. There is no false sentiment here, no anthropomorphism—it is sound natural history. Yet only an artist could have succeeded so well. The excellent wood-cuts are thoroughly in harmony with the spirit of the book.

Bentley Glass

Laboratory Manual for General Zoology.

By Tracy I. Storer. McGraw-Hill Book Company, Inc., New York and London. $1.25. viii + 150 pp. 1944.

Storer's manual is designed to accompany his "General Zoology." In accordance with the plan of this text, the manual is divided into two parts. The first part deals with animal biology in general, while the second consists of exercises on individual invertebrate forms. Most of the first part is on the anatomy of the frog which is treated quite comprehensively. In addition, there are exercises on such subjects as digestion, nervous responses, mitosis, embryology, heredity, ecology, etc. On the whole, the treatment of vertebrate physiology is very brief and is the weakest part of the manual. It seems unfortunate that the instructor has not been given greater latitude by the inclusion of more exercises on this subject. The organization of the individual exercises is excellent, and the format is in keeping with the high standards of the McGraw-Hill Publications in Zoological Sciences. Nevertheless, the manual represents no radical departure from the usual zoological course with its major emphasis on anatomy, but with a little physiology thrown in as though it were an afterthought.

Insects in Kansas. *Common Insects of Kansas. Report of the Kansas State Board of Agriculture, June, 1943. Volume LXII, No. 255.*

By Roger C. Smith, E. G. Kelly, George A. Dean, H. R. Bryson, and R. L. Parker. Kansas State Board of Agriculture, Topeka. Free upon request (paper). 440 pp. 1943.

This manual is one which will be useful far beyond the borders of Kansas. It has been prepared for the general public, and particularly for farmers, county agents, biology teachers in the public schools, boys and girls, and similar groups. It contains a great deal of information on useful and injurious insects, beekeeping (Parker), life cycles (Dean), and methods of collection (Bryson). A forty-page list of injurious insects (Kelly), describing in tabular form the nature of the injuries inflicted by them, their life cycles, and methods of prevention and control, and giving references to the figures and descriptions of the main section of the manual, should be especially useful. The bulk of the manual consists of descriptions of between 800 and 900 of the commonest, most important, or most typical Kansas species (Smith). These are arranged by orders and families, following Essig, with good figures of the great majority, and references to the taxonomic literature. There are six color plates, respectively of grasshoppers, the chinch bug, moths and butterflies, beetles (2), and bees. There is a full glossary and an adequate index. Keys are not provided.

The state of Kansas is to be congratulated on providing free for its citizens and others interested such a practical manual of insects.

Studies in Neotropical Mallophaga (III) [*Tinamidae No. 2*]. *Proceedings of the United States National Museum, Volume 95. Number 3180.*

By M. A. Carriker, Jr. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 81–233. 1944.

This is the second report on the lice of the tinamous by Carriker. The group is one of "highly diversified and specialized genera," with the two main divisions of the host family parasitized by "strikingly different types." The monograph describes 2 new genera, 15 new species, 68 new subspecies.

The Caddis Flies, or Trichoptera, of Illinois. *Bulletin of the Illinois Natural History Survey, Volume 23, Article 1.*

By Herbert H. Ross. State of Illinois, Department of Registration and Education, Natural History Survey Division, Urbana. $1.50 (paper). 326 pp. 1944.

Considering their close relationship to the Lepidoptera, the caddis-flies have in the past received surprisingly little attention. Betten's monograph on the Trichoptera of New York and the present one of Ross on those of Illinois elevate the group to its rightful place. This one, based on the collection of 750,000 specimens and the identification to species of no less than 150,000, raises the number of species recorded from Illinois from 37 to 183, and includes additional species from nearby regions which will probably be found in Illinois in the future. The immature stages of no less than 120 of these species are described. The biology and ecology of the group is discussed. Areas of distribution of representative species are mapped. Methods of collecting and preserving are described. The taxonomy is reviewed, and extensive revised keys to the families, genera, and species are given for adults, for pupae, and for larvae. There are concise descriptions and records of each species, with neotypes, holotypes, allotypes, and paratypes. The illustrations are outstanding, both the drawings of parts used, in identification, for their clarity, and those of the entire insects, larvae with or without cases as well as adults, for their delicate beauty. The illustrator, Dr. C. O. Mohr, deserves the highest commendation. The monograph ends with check list, bibliography, and index. It is unquestionably a most valuable contribution to insect taxonomy.

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INSECTS OF PORTO RICO AND THE VIRGIN ISLANDS

Lepidoptera (Suborder) Rhopalocera, (Superfamily) Papilionoidea (True Butterflies), (Superfamily) Hesperioidea (Skippers). Scientific Survey of Porto Rico and the Virgin Islands, Volume XII, Part 4.

By William Phillips Comstock. The New York Academy of Sciences, New York. $2.00 (paper). Pp. 421–622; 12 plates. 1944.

This survey of the butterflies of Porto Rico is based principally on the collections of the American Museum of Natural History and on two private collections. The arrangement follows that of the *Insecta Borinquensis*, by G. N. Wolcott. The check-list includes 110 species and subspecies, 97 of them personally confirmed. The bulk of the monograph consists of the descriptions of individual forms, including notes on the larvae, food plants, and occurrence. There is a key to the families represented. Numerous figures of venation are included, and many forms are illustrated in the rotogravure plates. The faunal distribution is discussed in a final section. There is an extensive bibliography but no index.

This monograph will be valuable not only to workers in the systematics of the Lepidoptera but also to students of zoogeography. It has every mark of a careful and thorough study.

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THE FISHES OF THE FAMILY CHARACINDAE FROM VENEZUELA, WITH DESCRIPTIONS OF SEVENTEEN NEW FORMS.

Proceedings of the United States National Museum, Volume 95. Number 3181.

By Leonard P. Schultz. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 235–367. 1944.

This monograph of Venezuelan freshwater fishes of the family Characinidae records 58 genera, and 117 species and subspecies, of which 3 genera and 17 species and sub-species are new. It is especially interesting that the forms of the Maracaibo Basin and of the Orinoco system are almost entirely different. Of 29 species from the Maracaibo Basin, for example, only 2 are known from the Orinoco system.

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THEY HOP AND CRAWL.

By Percy A. Morris. The Jaques Cattell Press, Lancaster. $3.50. xii + 253 pp. 1944.

In this unusually attractive book the author has given his readers a most interesting account of the life habits of the reptiles and amphibians found within the borders of the United States, especially those forms occurring east of the Mississippi. His wide field experience as naturalist and collector has given Morris the great advantage of being able to record first-hand facts and information. Throughout the text he emphasizes the fact that the majority of this country's cold-blooded animals are not only harmless and inoffensive but actually beneficial.

Approximately one half of the book is concerned with snakes, both harmless and poisonous types. This is not an undue proportion of the space when one considers the fascination with which mankind has always regarded the serpent. In view of the enormous amount of misinformation about snakes, the author has very appropriately included a chapter entitled "Snake Fallacies," in which he explains most of the strange myths which have no foundation whatsoever, yet are sincerely believed by a great many sensible people.

The text is bountifully illustrated with more than a hundred fine photographs of the various animals described, all taken in their natural surroundings. While written in particular for the amateur, the many attractive features of this book will also appeal to the more professionally minded reader.

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THE WAY BIRDS LIVE. *Second Edition.*

By Edward A. Armstrong. Lindsay Drummond Ltd., London. 7s. 6d. 96 pp.; 16 plates. 1944.

Intended primarily for children, this little book will prove worth-while reading for any amateur ornithologist. The manner of mate attraction and selection, the various types of adornment and their use in display, courtship gifts and feedings, and other kinds of behavior prior to egg laying are briefly described. The story continues by telling of the eggs, the young, their hatching, and their powers of learning versus their inborn knowledge. Communal behavior, roosting, food, migration, and pointers on methods of bird watching complete the book Photographs and sketches by the writer illustrate the various activities of the birds. Although the discussions are very short, they provide a preliminary background to certain aspects of bird life usually missing in most handbooks.

HENRI SEIBERT

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SOMERSET BIRDS AND SOME OTHER FOLK.

By E. W. Hendy with an introduction by H. J. Massingham. Eyre and Spottiswoode, London. 12s. 6d. 165 pp.; 15 plates. 1944.

Without doubt, this book is well written and some of the vivid descriptions of moor and marsh are expertly rendered. The subject, as stated in the foreword, "... tells of my experiences with the birds of Exmoor and the Somerset countryside but also has something to say about other country creatures, human and unhuman."

Ornithologically, it leaves much to be desired, for the writer has sacrificed valuable data for the sake of fluidity of prose. Be that as it may, the chapters on the chaffinch, the merlin, the robin, and other denizens in and around Porlock contain informative material, much of it obtained by banding. Emphasis is repeatedly placed on observations in the field as the only way to learn about birds, yet apparently Hendy has the feeling that this is a method scorned by ornithologists. "Modern ornithology appears more and more to aim at reducing fieldwork to an elaborate system of census making and card indexing by teams of workers." (p. 63). There is a similar statement on p. 108. Further criticism is leveled at modern ornithologists, "against the 'intensive and American' methods of some modern ornithologists," because "these 'highly specialised programmes' tend to convert what is really a sport or recreation into 'a ruthless business proposition'." Nor does the author have a high regard for the professionals for refusing to accept certain sight records of rare birds.

The ancient controversy as to whether the female adder swallows her young is reopened, and whereas the writer does not commit himself one way or the other, he finds it difficult to believe that all eye-witness accounts are illusions, and so prefers to keep an open mind.

The photographs are excellent.

HENRI SEIBERT

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THE BIRDS OF TIMOR AND SUMBA. *Bulletin of the American Museum of Natural History, Volume 83: Article 2.*

By Ernst Mayr. American Museum of Natural History, New York. 65 cents (paper). Pp. 123–194. 1944.

This check list is based on the collections made on Timor and Sumba by Georg Stein, with additional species collected by others included in the list to complete the compilation. Taxonomic notes on the birds of both islands follow the annotations. This section provides critical reviews of genera and of certain groups whose exact relationships have long been taxonomic puzzles. Many new subspecies are described.

The remainder of the report is devoted to the zoogeography of the two islands. On the basis of the composition of its avifauna, Timor is found to belong more closely to the Oriental than to the Australo-Papuan region. Ornithologically it is most nearly related to Wetar, although separated from that island by a deep channel. The land bridges claimed by Rensch to have existed between Timor and Sumba, Timor and Wetar, Timor and Celebes, etc., are disproved on the basis of the avian distribution. Mayr furthermore concludes with Wallace that Timor and Australia were never connected by land, although separated at one time by a strait of only 20 to 40 miles in width. The dispersal faculties of birds are thus emphasized, and distribution is made to fit more closely with geological evidence. The birds of Sumba are most similar to those of Flores and are considered as being derived from the Lombok-Alor chain.

HENRI SEIBERT

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THE WOLVES OF MOUNT MCKINLEY. *Fauna of the National Parks of the United States—Fauna Series No. 5.*

By Adolph Murie. United States Department of the Interior, National Park Service; U. S. Government Printing Office, Washington. 40 cents (paper). xx + 238 pp. 1944.

This is an exemplary report on an extensive field study of the life histories and ecological conditions of the larger animals in the Mount McKinley National Park. Special attention is paid to the timber wolf (*Canis lupus pambasileus*) and the Dall sheep (*Ovis dalli dalli*), inhabiting the slopes of the highest mountain in North America, since the author had originally been requested to investigate the relationships between these two animals to determine the influence of the wolf predators on the number of sheep. It is very gratifying that the book has been expanded to include also accounts of the caribou, moose, grizzly bear, fox, and eagle in the same park area. The entire complex problem of the factors underlying the density of a wild animal population and the ceaseless struggle for survival has been considered in a thorough and informative manner, using wolf and sheep as special examples. Careful records on feeding and breeding habits, on the effect of climatic changes, on the prevalence of disease and its correlation with the age of the animals, etc., are enlivened by relevant accounts of specific incidents observed in the field.

Wolves prey chiefly on caribou, to a lesser extent on sheep and least of all on moose. Of sheep, only the young in their first year and old or diseased animals are killed. The golden eagle attacks young sheep very rarely, and the grizzly feeds on the ungulates mostly in form of carrion only. It is concluded that in this park area a normal prey-predator adjustment has been attained.

The report is illustrated with 58 excellent photographs and drawings, which alone are well worth the remarkably modest price of this splendid publication.

ADOLPH H. SCHULTZ

THE NATURAL HISTORY AND BEHAVIOR OF THE WESTERN CHIPMUNK AND THE MANTLED GROUND SQUIRREL.

By Kenneth Gordon. Oregon State College Press Corvallis. 75 cents (paper). 104 pp. 1943.

This monograph, illustrated with attractive sketches by the author, considers in as complete a fashion as possible the biology of *Eutamias* and *Citellus lateralis*. The author has studied these little rodents extensively and over a period of years. He includes sections on taxonomy, description, distribution, biology (movements, dens, food, water, reproduction), ecology (environmental factors and reactions, community organization, population, economic relations), and behavior (sensory, reactive, and modifiable). Like the observations of social dominance, the experiments with mazes, problem boxes, and strings on aspects of learning, retention, and individuality are most interesting because, although not sufficiently extensive, they were conducted in the field on wild, and not on captive, animals. Gordon concludes by pointing out the numerous questions still to be answered regarding these relatively much observed and familiar mammals.

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RAYMOND L. DITMARS. *His Exciting Career with Reptiles, Animals and Insects.*

By L. N. Wood. Julian Messner, Inc., New York. $2.50. 8¾ x 6. x + 272. 1944.

This volume is another of the Julian Messner shelf of modern narrative biographies created to satisfy a desire among librarians, parents, teachers, and intelligent readers for really authoritative biographies of characters of interest for this generation. While the present recreation of the life of Raymond Ditmars is an award book of the Julia Ellsworth Ford Foundation for children's literature, adults as well as younger readers will find it unusually entertaining reading. As one reviewer has already commented, it does for the reader what Ditmars himself did for the public—makes snakes popular and understood as interesting creatures.

Raymond Ditmars was indeed a confirmed nature-lover. Early in life, we are told, he exhibited interest in all sorts of living things, particularly snakes, to such an unusual degree that even his own family regarded him as somewhat of a problem. When, at the age of seventeen, Dr. Beutenmuller of the American Museum of Natural History offered him a job as assistant, young Raymond was almost too overcome to answer. To his dismay, his parents were cool to the idea. Mounting butterflies at the museum might be pleasant work for a couple of months in the summer, but what prospect did it offer for a career. No one had ever made a success of life just by chasing butterflies and snakes!

From his associations at the Museum with such outstanding men as Chapman, Osborn, Gratacap, Beutenmuller and others, Ditmars learned a great deal besides responsibility and system. The encouragement and friendship which they gave him really launched him into his career as a scientist.

In the year 1899, at the age of 23, the one perfect job in the world for him came when he was asked to become curator of reptiles at the New York Zoological Park. Preparations were being made for the opening of the Park on the 261 acres of wilderness at the southern end of Bronx Park. Although the Reptile House was not yet completed, Ditmars, as soon as he joined the staff of the zoo, set to work to form a collection, with his own private collection of forty-five snakes representing fifteen species as a nucleus. Up until this time his very valuable collection had been housed on the top floor of the parental brownstone mansion in the Bronx. The young curator's primary concern in his new job was to expand the collection. He succeeded in this so well that by the first year he had acquired more than 400 reptiles. Under his expert management the reptile house became so entirely satisfactory to the public and to the directors that he was soon asked to take over the mammals as well. His relentless search for new and rare specimens took him to the far corners of the earth. The present volume records many extremely interesting and amusing incidents which occurred during these numerous and varied expeditions.

There can be no doubt that Ditmars had a happy flair for popular education. His numerous books were designed both to amuse and inform. Throughout his life he waged a campaign to arouse popular sympathy towards all forms of animal life, including those usually regarded as "repulsive."

That he succeeded very well in changing the attitude of the public is indicated by an editorial in one of the leading metropolitan newspapers in the spring of 1937, just 30 years after the publication of *The Reptile Book*, which hailed the beginning of the snake-hunting season with the statement "... snake hunts are growing positively popular ...." Uncritical shudders at reptiles were giving place to intelligent interest in them. The day of the editor, once known to Ditmars, who had rejected the manuscript of a stoıy about a snake by throwing it on the floor and jumping on it, was past.

MARY E. RAWLES

ANIMAL EMBRYOLOGY

OURSELVES UNBORN: *An Embryologist's Essay On Man. The Terry Lectures.*

By George W. Corner. Yale University Press, New Haven. $3.00. xiv + 188 pp.; 8 plates. 1944.

Corner has chosen, in the Terry Foundation Lectures "on Religion in the Light of Science and Philosophy," to apotheosize the human embryo in a triptych, the panels of which portray respectively (1) the essential morphological and physiological aspects of normal human development, (2) the nature of the misfortunes which can befall the human embryo during its development, and (3) the relationship of man to the other brutes as elucidated by the known facts of human development and placentation.

In his first essay, Corner has professed to cover the early developmental history of the human embryo as "an archive in which is written the evidence of its descent as an animal, a vertebrate, an amniote, a mammal, a primate." He has included in his review a brief schematization of the conventionalized pattern to which mammalian development can be reduced; a description, surprisingly but agreeably detailed for a popular treatise, of the method of separation of the so-called germ-layers and auxiliary membranes in the primate embryo; and an analysis of the relationship of the embryo to its uterine environment. In the second essay, the author has described and treated of various abnormalities of human development, ranging from local deformities through faulty implantation to erythroblastosis fetalis. In his final essay he has discussed first the historical development of the concept of evolution, next the modern anatomical and paleontological foundations for the classification of mammals and primates, and finally the light which embryology sheds on the position of man among his fellow-creatures.

Especially commendable is his success in relating the facts of embryology to those of evolution. His emphasis on the qualities of the primates as a generalized rather than a specialized group is particularly welcome in a book designed for popular consumption, as is his interpretation of the biogenetic law "To say that the pharyngeal bars suggest a common origin for fish and man," states Corner on page 67, "is a very different thing from claiming that as embryos we humans have gills and therefore we must have had a fish for a direct ancestor." A very different thing it is indeed, but all too many workers even in this age drift into the more careless Haeckelian habit of thought or expression, and unfortunately in material presented to the serious student as well as to the general reader. Popularization of the sounder and more critical evaluation cannot fail to be salutary in a book destined for as wide dissemination as the present one.

The volume suffers to a certain extent from a lack of homogeneity in form. The author's exposition throughout is simple, straightforward, and admittedly everywhere lucid. But if at best his style aspires to the sonorousness of the rolling phrases of the Prophets, at its poorest it becomes vitiated by utterances more properly befitting the Philistines. One could wish that the author had indulged in more careful editing, for the purpose of ataining a higher degree of uniformity of expression.

The volume exhibits also some unevenness in content. The present reviewer wonders, for instance, whether the necessarily somewhat technical discussion of the immunological basis of erythroblastosis fetalis can be appreciated by the same reader for whom Corner has labored at length to lay the spectre of prenatal influence. The question arises, indeed, as to how easily many of the included materials, even with the benefit of Corner's excellent clarification of details, are assimilable by an audience unfamiliar alike with the facts, the methods, and the terminology of biological science. For the student already conversant with these materials, however, the volume provides an admirable summary of the data at hand.

JANE OPPENHEIMER

A LABORATORY MANUAL OF VERTEBRATE EMBRYOLOGY. *Revised.*

By Roberts Rugh. Burgess Publishing Company, Minneapolis. $2.00 (paper). x + 194 pp. 1944.

This manual sets a new high standard in the extent and completeness of material covered, in number and general excellence of illustrations, and in fullness of text. Indeed, by a process analogous to the one that has made destroyers in this war the size of cruisers in the last, and cruisers the size of battleships, this is a laboratory manual that has become a textbook, as was intended, largely on the descriptive level.

The bulk of the material, quite rightly, concerns the frog, chick, and pig, but there are sections on the general aspects of gametogenesis, fertilization, and cleavage. Conklin's figures of the development of *Amphioxus* have been reproduced from the *Journal of Morphology*. Directions, drawings, and photographs for the study of the early development of *Oryzias*, the Medaka fish, should prove extremely valuable as this practical, laboratory-breeding teleost comes into general use. Each section is followed by a dozen or so review questions and page assignments in standard texts. There are numerous blank spaces for student's drawings and numerous drawings for labelling. Give the students their slides and this manual, and the laboratory will largely run itself.

The chief general criticism—entirely a matter of policy—is that the manual deals almost exclusively with prepared slides. The embryologist who believes it important for students to roll up their sleeves and work with fresh material, to dissect amphibian blastulas under a binocular microscope, to remove from the egg and prepare their own whole mounts of chick embryos, or otherwise to manipulate embryological material will have to supplement. The manual is so arranged that this can be done.

Several minor faults can easily be remedied in subsequent issues. The section on meiosis is outdated and should be rewritten. The 43 photographs of frog development, admirable as they are, still do not show all the structures mentioned in the legends and could be sharper. When such a series of photographs is presented, would not the permanent usefulness of any manual be greatly enhanced if they tallied with standard stages of development—in this case with the stages given for *Rana pipiens* by Shumway? The term blastopore is introduced almost casually while some lesser terms are fully explained. Various figures from Patten are reproduced effectively and with full acknowledgment. At least half a dozen others that have been redrawn with only the most trivial changes should also have been accompanied by acknowledgments. These are, however, minor faults in an outstanding, competent piece of work.

G. B. Moment

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ANIMAL MORPHOLOGY

A Textbook of Histology. *Functional Significance of Cells and Intercellular Substances. Third Edition.*
By E. V. Cowdry. Lea & Febiger, Philadelphia. $7.00. 426 pp. 1944.

This new edition is not, as are so many revisions of successful texts, an expansion of the original. The effort has been made, and very successfully, to reduce the detailed treatment, to give a stronger emphasis to fundamentals, to focus "attention on the correlation of form and function." As in the earlier editions, the presentation centers around the blood vascular system and the fluid environment of the cells as the principal integrator, and a dynamic view of cellular integration and activity results. Still less than before is this text to be compared with such texts as Maximow and Bloom's. Those who want an exhaustively illustrated book that can be used as a reference in later work will still prefer the latter type. Those who are interested in cell differentiation and embryological histology will also have to look elsewhere. But those who want a simple and dynamic picture of correlated form and function, with half as many figures and far fewer in color, will prefer Cowdry's book. (One should note that the reduction in illustration is not accompanied by a lower price). For the elementary student of the subject, this should be an excellent guide.

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ANIMAL PHYSIOLOGY

Fundamentals of Physiology. *The Human Body: Its Functions and Structure.*
By Elbert Tokay. The New Home Library, The Blakiston Company, Philadelphia. 69 cents. xiv + 336 pp. 1944.

This volume is advertised as "a book which explains clearly the important things you need to know about the structure and function of the human body." The author has succeeded in giving a clear and simple description of the structures of the body and their function. The properties of living matter and the organization of the body are described in introductory chapters. These are followed by discussions of the circulatory, respiratory, digestive, excretory, endocrine, neuro-muscular, and reproductive systems. The final chapters of the book are devoted to a consideration of nutrition, metabolism, exercise, protection against disease, and the health of the body. Thus, many aspects of physiology have been touched upon, but one cannot say that this review contains all the facts one needs to know. There are a few bad mistakes, such as a faulty description of the mechanism of function of the carotid sinus, but on the whole the volume is a very creditable contribution to a set of books which is being published for the layman. The book, however, does not deserve the serious attention of students of medicine or advanced students of the biological sciences. They require a somewhat closer approach to the true and complex picture of physiological functions than the publishers and the author of this book seem to feel is desired by laymen. Many of the 150 illustrations specially prepared are adequate, but quite a few contribute little, and some are incorrect. For example, the diagram of the cerebellum on page 190 is oversimplified and labeled incorrectly; figure 108 is unnecessarily poor; figure 112 omits certain functionally important peculiarities of the thoraco-lumbar division of the autonomic system. The chief feature which recommends this book is its clarity, and those whose requirements are not great may find it to be completely satisfactory.

Chandler McC. Brooks

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Chemical Anatomy, Physiology and Pathology of Extracellular Fluid. *A Lecture Syllabus. Fourth Edition.*
By James L. Gamble. Department of Pediatrics, The Harvard Medical School, Cambridge. 75 cents (paper). 46 charts with text. 1942.

This is a reprinting of the fourth edition of a lecture syllabus which has become a standard work in physiology. It consists of a series of 47 charts and accompanying descriptions dealing with the volume, composition, and changes which may occur in the plasma and interstitial fluid constituting the aqueous environment of body cells. The various topics treated are: the role of extracellular fluid in regulatory reactions, the participation of the fluid in osmotic adjustments, the renal defense of the chemical structure of body fluids, the regulation of extracellular fluid volume, the pathogenesis of dehydration, acidosis and alkalosis, and the rationale of replacement therapy. This concise, yet thorough, discussion of the stability of the internal environment of the body cells is highly recommended to those physiologists and physiological chemists who are not already familiar with this work.

Chandler McC. Brooks

FEMALE ENDOCRINOLOGY *Including Sections on the Male.*
By Jacob Hoffman. W. B. Saunders Company, Philadelphia; London. $10.00. xv + 788 pp. 1944.

This volume is a careful and thorough handbook, setting forth the pathology, diagnosis, and treatment of endocrine disturbances of the reproductive system and of related diseases. Its teaching is based on a full review of current knowledge about the physiology of reproduction in mammals. The text is clear and well arranged. Full, up-to-date reference lists are provided. The book will be useful to teachers of physiology as well as to clinicians and medical students. Its readers may find themselves at times wishing for more of the savor of personal experience. Hoffman, who in fact has had considerable experience as experimentalist, pathologist, and practitioner, reviews his topics with such painstaking care that his own judgments and conjectures do not always come to the surface. Soundness on a subject like this, however, may be at the present time preferable to individuality.

GEORGE W. CORNER

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NEUROLOGY OF THE EYE, EAR, NOSE, AND THROAT.
By E. A. Spiegel and I. Sommer. Grune and Stratton, New York. $7.50. xi + 667 pp. 1944.

This volume is intended as a survey of the present state of knowledge in the "borderland" between neurology and otolaryngology and ophthalmology. It succeeds in being an excellent approach toward a greater synthesis in the teaching of these fields of medicine. Aberrations of the special sensory and motor functions associated with the apertures of the head cannot be understood without a background of cerebral anatomy and physiology, just as these subjects are intelligible only when considered in relation to peripheral functions. The authors present a unified account of the functions and dysfunctions of the eye, ear, nose, and throat, and their associated cranial nerves and cerebral structures. Discussions include highlights of modern investigative results, and are obviously tempered by long experience in research, teaching, and clinical practice. As an attempt to cover the fields of anatomical and physiological fundamentals, pathophysiology, modern experimental research, clinical practice, and therapy, the text of six hundred odd pages is often synoptic. It is debatable whether or not the theme of unity is weakened by setting apart two final chapters as a brief review of the symptomatology of brain stem and cortex. The reviewer, for example, would have preferred where possible a complete integration of this material with the rest of the book. In view of the excellence of many of the illustrations, the crude execution of others, especially some of the line diagrams, is surprising. An extensive bibliography is appended. The book should be of interest and value to practitioners and advanced students in the specialties of ophthalmology, otolaryngology, and neurology.

DAVID BODIAN

HEALTH AND DISEASE

FOUNDATIONS FOR LIVING.
By Fern Silver and Mildred Graves Ryan. D. Appleton-Century Company, New York. $2.12. x + 615 pp. 1943.

Although the aim of modern education has been carefully defined in terms of preparation for worth-while living, very few text books have been published with that aim as clearly in view as the present one. The volume is designed for use as a senior high school text in home economics courses, but it covers such a wide variety of topics in addition to the time honored principles of cooking and sewing, that it is truly a guide to at least one fundamental element of worth-while living: namely, intelligent, economic, and enjoyable homemaking.

The authors have broken through the stiff crust of accepted pedagogy, and have discussed, in the very first section of the book, such modern, yet practical, topics as boy and girl relationships, sex, courtship, marriage, good manners, and finding a job, all under the general heading of personal and social relationships. This section is not just a conglomerate mixture of Dorothy Dix and Emily Post, but rather a guide for intelligent young people in solving some of their most vital personal problems *now*, by some method other than that of trial and error.

In the next four sections, attention is directed to such practical yet fundamental factors in living as foods, clothing, personal appearance, and home management. No effort has been spared here in presenting sound, common-sense facts in a completely authentic, yet thoroughly understandable manner. Two particularly helpful sections covering consumer buying and home furnishing and care have been included. Under consumer buying the authors have presented a wealth of material dealing with the selection and purchase of a variety of products ranging from meats, canned goods, eggs and milk, to clothes and shoes. The final section on child care and guidance rounds out a well balanced and carefully prepared course of study that should contribute in no small manner to the successful home-making endeavors of its users.

The many graphic and photographic illustrations, as well as the chapter references and complete index, enhance the value of the text for either class-room or home use.

B. AUBREY SCHNEIDER

TO LIVE IN HEALTH.

By R. Will Burnett. Duell, Sloan and Pearce, New York. $2.75. vii + 332 pp. 1944.

The underlying principle and constant theme of this excellent work is the expression of a deep conviction that the practice of sound health habits can come only as a result of sound knowledge of scientific health facts. It has been the author's purpose to make available to the lay reader, in clear, non-technical language, a body of scientifically accurate facts concerning both personal and public health as related to the welfare of the nation.

Since the human body is the central figure in any consideration of personal or public health, much of the volume has been devoted to discussions of the common causes of death and disability in the American population, the performances of the body in warding off its common health enemies, and the physiological reactions of the human system in recovering from the ravages of disease and injury.

Wherever the opportunity presents itself, the author has used scientific facts to dispel common superstitions and false conceptions concerning the principles and practice of healthful living habits. The outstanding advances in our knowledge of bacteriology, immunology, parasitology, and nutrition over the past one hundred years have been presented in a popular, yet completely authentic manner.

The careful selection and logical presentation of the material will make the volume serve well for use in senior high school or college courses in health and hygiene, as well as in the home library. Many graphic and photographic illustrations are used in clarifying the general health problem of the nation.

An index and a list of preferred references relating to each chapter are appended.

B. AUBREY SCHNEIDER

AN INTRODUCTION TO PUBLIC HEALTH. *Second Edition.*

By Harry S. Mustard. The Macmillan Company, New York. $3.25. ix + 283 pp. 1944.

The materials and methods associated with the general field of public health have been clearly outlined in this superb text, which is designed especially for use in medical schools, nursing schools, general college courses in hygiene, and as an introductory course for regular students of public health. As in the previous edition, the discussions are largely devoted to the definition of public health terms and problems, and analyses of the purposes and methods of protecting the health and caring for the illnesses of the general population.

The chapters on communicable diseases have been revised to include the latest knowledge in the fields of bacteriology, immunology, viruses, and chemotherapy. The sudden impact of war-time living and working has introduced many new problems in the general public health picture in the United States; hence the present edition has incorporated new chapters on industrial hygiene and medical care.

Some readers may be irritated by the numbered-item, outline method of presentation; however, the overworked student will find this method very convenient for purposes of review or reference. Although the text is completely devoid of charts, graphs, or diagrams, and the tabular material is very meager, the work is thoroughly documented, and each chapter is concluded with a select list of references. An index is provided.

B. AUBREY SCHNEIDER

ESSAYS IN THE HISTORY OF MEDICINE *Presented to Professor Arturo Castiglioni on the Occasion of his Seventieth Birthday, April 10, 1944. Supplements to the Bulletin of the History of Medicine Number 3.*

Edited by Henry E. Sigerist and Genevieve Miller. The Johns Hopkins Press, Baltimore. $3.50 (paper). vi + 358 pp. 1944.

Generally there is not much ado over the anniversaries of the aging refugee scholar, cut off from his pupils and friends. Arturo Castiglioni, former professor of the history of medicine at Padua, and now connected with Yale University, has happily escaped this fate. On the occasion of his seventieth birthday he has been presented with this quite substantial volume, containing not less than 26 contributions in 6 different languages. This "Festschrift" bears witness to the general esteem in which Castiglioni, the man and the scholar, the author of a widely read and translated one-volume history of medicine, and of numerous studies covering especially the Renaissance period and magic in medicine, is held even outside of his unfortunate country.

None of the contributions of this volume deals with magic, while three papers concerned with Renaissance personalities and problems are among the tastiest slices of Castiglioni's birthday cake (J. F. Fulton, "Polydore Vergil"; C. F. Mayer, "Mignotydea"; C. Proskauer, "Der Zahnbrecher des Hans Sachs"). Iago Galdston and G. Sarton contribute two very attractive sketches of eighteenth century scientists, Ozanam and Beccaria. E. B. Krumbhaar-W. B. McDaniel's "Angina inflammatoria as described in David Orme's Edinburgh Dissertation (1749) and Benjamin Morris' Leyden Dissertation (1750)" and A. Magnus-Levy's "Diabetikerdiäten der Vorinsulinära" deal very competently with special chapters in the history of the actual practice of medicine. It is the reviewer's opinion that the future of the history of medicine as a living science depends directly on an increase of this type of study, which at present unfortunately is the Cinderella of medical historiography. G. Urdang's "Retail Pharmacy as the Nucleus of Pharmaceutical Industry" will be studied with great profit.

Particularly numerous throughout the volume are the contributions from Latin America. Most enjoyable is C. E. Paz Soldan's "Medidas de Seguridad contra la Fiebre Amarilla durante el Virreynato del Peru." North Americans will be glad to have J. B. Lastres' stimulating essay on "Medicina Aborigen Peruana," published a few years ago in Peru, now easily accessible in a North American publication. Carlos Martinez Duran, well known for his work on the history of hospitals in Latin America, gives an interesting survey on "Los Hospitales de América durante la Epoca Colonial." Nevertheless, the reviewer feels that Duran's evaluation of the Spanish Conquest in general as an essentially spiritual phenomenon and his unrestrained praise of a type of hospital more often created as a soul-trap for dying heathen than as a medical institution, is at least open to discussion.

Leonardo Olschki's "Medical Matters in Marco Polo's Description of the World" is perhaps the most fascinating piece among so many other interesting papers.

The reviewer, being unable even to enumerate more than a minority among the 26 contributions, is painfully aware of the arbitrariness of his procedure. He is certain that competent readers will find among the essays unmentioned not only several they will judge equal, but may even prefer to those discussed.

ERWIN H. ACKERKNECHT

THE ART OF THE HEALER.

By Bernard Aschner. Translated by Ruth and Heinz Norden. The Dial Press, New York. $2.75. viii + 306 pp. 1942.

Bernard Aschner began his career as a brilliant experimentalist. He was the first to remove the entire pituitary gland from a dog, and thereby to demonstrate the control of the gland over normal growth. He also showed that it was related to carbohydrate metabolism. And he discovered the oculo-cardiac reflex. In Europe he was well-known as a gynecologist and student of medical history. He is therefore entitled to respectful attention when he writes on healing.

His main thesis is provocative, and, to a degree, it is sound enough. Medicine, he thinks, has been so dazzled by the modern achievements of experimental science that it has unduly neglected the time-tested values of the medical knowledge of earlier times, and of the common folk. Here readers are in for their first shock. It is not the rise of bacteriology and the germ theory of disease that Aschner has in mind—these are scarcely mentioned in the entire book. The real villains of the piece are Bichat and von Virchow, who were responsible for the emphasis upon cellular pathology and diagnosis. Back to the Golden Age of medicine!—to the days when doctors like Boerhaave, Sydenham, and Hufeland followed Plato's dictum that "Good physicians apply their treatment to the whole body and attempt to heal the sick part or organ by treating the whole individual." This is Aschner's Constitutional Therapy. Early in his career, he determined not to ignore the heritage of the past.

Now it is true, as Sigerist has said, that "experience has preceded science more than once." But this is not to say that the lore of the past is not to be retested by scientific means before retention or rejection. Aschner, however, as he became more learned in medical history, seems to have become less critical of ancient beliefs regarding medical virtue and less aware of contradictory evidence from scientific experiment. He revives the ancient theory of the four humors and the use of counter-irritants. He calls for leeches, venesection, purges and emetics, hydrotherapy, sweating, and other devices for detoxicating the system. There can be little doubt that some of these treatments may in certain cases be helpful. But Aschner neither establishes statistical proof nor cares for experimental verification. Treatments are efficacious because Galen, or Paracelsus, or perchance Hippocrates, recommended them. In our author's hands, medicine becomes an art based on intuition, no longer a science.

As a result, all varieties of questionable statement and clear error abound. What is one to think of remarks such as these: "Meat, spices, and alcohol tend to make the individual 'hot-blooded' "; "overfeeding with a milk and gruel diet makes the stomach lazy and provokes hyperacidity. Forcing [children] to drink a pint and even a quart of milk a day thus greatly contributes to frequent tonsillitis"; "... conclusions as to constitution, character, intellectual capacity, and temperament may be drawn from a man's nasal configuration"; "a large mouth indicates greater vital energy"; "the female body ... certainly is not as strongly differentiated from the body of the child as is the male body"; "menstruation is ... a purge of the whole system"; "the cleansing of the body by skin respiration"? Aschner cites with approval the drugs recommended by Paracelsus for prolonging life—by Paracelsus, who lived 48 years. He speaks believingly of the extraordinary longevity of the Chinese. He is sure that the moon has a profound cosmic influence on women which it is superstition to deny. And all his beliefs are stated as facts.

Every page will evoke similar criticism. This book will undoubtedly be most pernicious in the hands of the general public. Read by doctors and biologists who can discern the false, it may have a wholesome corrective influence, like one of Aschner's own purges or emetics.

BENTLEY GLASS

SOMETHING NEW ABOUT HEALTH AND HEALING.

By P. F. Van Den Daele. The Christopher Publishing House, Boston. $3.00. 288 pp. 1944.

The author of this treatise signs himself B. S. This stands—not for what you suppose—but for Bloodless Surgeon. Hailing, apparently, from Boston, he makes one wonder just what the requirements for practising medicine in Massachusetts can possibly be, or whether they are enforced. Van Den Daele has a number of sensible ideas, he has picked up a considerable amount of standard medical knowledge, but one does not have to read far to run into such wonderful bits of anatomical lore as the following: "When the appendix becomes infected, the abdominal membrane, called the peritoneum, folds itself around the appendix and isolates it from other structures. This prevents deadly peritonitis. If, however, the patient eats, or even worse takes laxatives, the action of the peritoneum immediately stops . . ." The author thinks "streptococcus is so harmful and . . . staphylococcus is comparatively harmless" because "the one is the *cause*, the other is the *result* of infection." In spite of this conclusion, he later considers he has discovered a number of points fatal to the "germ" theory of disease.

The following story is so touchingly told that it must be related in full:

> I often think of a once happy family—father, mother and a most promising son. He was working for a concern whose president had great plans for him. The firm had already placed him at the head of his department and had decided to build a larger office for him. At that time there were some cases of diphtheria, and the boy asked me if he should take some "shots" for it. I advised him against it. I warned him that his heart, glands and general condition would suffer. I explained that it would be better to take normal health precautions. The company doctor, however, talked him into taking an antitoxin. About half a year later, the mother called me and related a sad story. The boy had changed entirely. He had become lazy, difficult to handle, and very wild. His superiors in the office had to demote him, and finally they had been compelled to actually discharge him. I waited for him to come home and then examined him. I found a wretched constitution, a weakened heart, and an irritable disposition resulting from his general condition. Later on, he became a "bootlegger," was caught and sent to prison. Both his parents died with a broken heart. This is a sad example of one who did things to his body without first investigating honestly what the after affects would be to his heart and glands.

The bloodless surgeon makes use of all sorts of treatments, from massage and chiropractic to hydrotherapy and bloodless surgery itself. The latter is credited with numerous cures of appendicitis, peritonitis, gall stones, and tumors, among other troubles, but just what it is, other than "corrective manipulations," is not explained. The list of cures is not relieved by any record of the number of patients the worthy doctor has killed.

This book is highly recommended to biologists on two grounds. It will strengthen their realization of the need for constant public education in matters of health and disease and for an active effort to raise and enforce the standards of medical licensing. Besides which, it is a masterpiece of unconscious humor.

BENTLEY GLASS

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DEAFNESS AND THE DEAF IN THE UNITED STATES *Considered Primarily in Relation to Those Sometimes More or Less Erroneously Known as "Deaf-mutes."*

By Harry Best. The Macmillan Company, New York. $6.50. xix + 675 pp. 1943.

The anticipation with which the reviewer opened this thick volume on a topic long of interest to him soon turned to disappointment. The first chapter, entitled "Causes of Deafness," is the one the reviewer is best qualified to judge. A large portion of this chapter, as also of several other chapters, consists of tabulations copied from U. S. census reports and textual repetitions of the data in the tables. In almost all instances, percentage rather than numerical figures are the only ones given. The author does not treat the data critically; furthermore, he repeats ideas long since discredited and seems to know but little about the anatomy of the organ of hearing. Certainly the chapter adds nothing to knowledge of the topic.

The six-page bibliography appended to Chapter I is not arranged alphabetically or chronologically. Numerous items give neither the name of the author nor the title of the paper and are identified merely by name of journal, volume, page, and year. Many clinical textbooks, old as well as recent ones, are included, and also a number of articles in popular magazines. The text contains no references to the items listed in the bibliography.

A geneticist who read the chapter on Heredity of Deafness was similarly disappointed in the treatment of that topic. Perhaps the sections of the book that deal with educational, economic, and social problems of the deaf are better than are those on biologic aspects of deafness, but the impression gained by the reviewer, from a hasty perusal of these sections, leads him to believe specialists in these fields also will be disappointed with this book.

The tone of the author's treatment of his topic is indicated by the following excerpts:

> p. 4, "The apparatus as a whole is a highly involved and complicated one, with its passageways, tubes, cavities, walls, partitions, fibres, and compact or solidified matter, all linked together in a finely coördinated but riveted connection." p. 388, "But the day of deliverance was at hand." p. 622, "It is high time in the history of the world that an end should be put to views that differentiate the deaf from the rest of their kind, or stigmatize or debase them. Too long have they had to suffer from misunderstandings, misapprehensions, misconceptions. Great will be their rejoicing when they receive in this respect only what is their due."

STACY R. GUILD

Elimination Diets and the Patient's Allergies. *A Handbook of Allergy.*

By Albert H. Rowe. Lea and Febiger, Philadelphia. $3.50. 256 pp. 1944.

This book is a brief resumé of allergic diseases. The first 130 pages are devoted to a critical review of the methods of diagnosis and the causes of allergy and their control. The balance of the book, 120 pages, is devoted to elimination diets. The style of the writing is rather stilted, as might be expected in a manual.

As the author is primarily concerned with foods and their relation to allergy, it is only natural that his interest should influence his discussion of other possible causes of allergic diseases. To any physician who is a disciple of Rowe, I am sure that this publication will be very helpful in the preparation of menus for patients suspected of having some food sensitivity. As the reviewer does not agree with the opinion that food plays such a major role in allergic diseases, excepting in infants, young children, and a small proportion of adults, it is natural that the opinion expressed is critical.

The manual is written with such didactic positiveness that one who is inexperienced might accept "food allergy" with the belief that the hypothetical discussions were backed by scientific proof; that the majority of human mortals are victims of one or more "food sensitivities." Unfortunately, the tendency toward a broad interpretation of the definition of allergy, accompanied by reports of cases inadequately studied and not followed for a sufficient period of time, has frequently led to undue emphasis upon the prevalence of food allergy.

It is unfortunate that allergists rarely consider the psychosomatic side of human behavior; careful laboratory studies of the gastrointestinal tract are often overlooked. Treatment of these important phases of medical disease frequently relieve the patient of his symptoms. Unfortunately, this is not the fault of the patient. He goes to his physician because of numerous digestive symptoms, and, if the medical advisor is an allergist, often "food sensitivity" is suspected as the cause of the discomfort. For a time the patient accepts such an opinion; then his symptoms, temporarily relieved, return, and permanent relief is obtained when a thorough study of his home environment and of his many mental problems is made, and when these all-important factors are adjusted.

Acceptance of Rowe's opinion unfortunately leads to errors in diagnosis, and while he is most sincere in his beliefs, the reviewer does not whole-heartedly accept them. The latter half of his book could be considerably curtailed.

Leslie N. Gay

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Cancer: *A Study for Laymen. Prepared for the Women's Field Army of The American Society for the Control of Cancer, Inc.*

Edited by Clarence C. Little. Farrar and Rinehart, Inc., New York and Toronto. Paper. 122 pp.; 2 plates. 1944.

For workers in public education on the subject of cancer this fine informative and non-technical treatment has been prepared by a corps of specialists. The first section deals with the spirit, methods, and fundamental principles of general biological research. In 46 pages a remarkably complete background for understanding the cancer problem has been provided by C. C. Little. Section II, Diagnosis and Treatment, contains brief introductory topics on the lymphatics (Florence R. Sabin), the preparation of tissue for microscopic study (Little), cancer hospitals (James Ewing), x-rays and radium (Edith Quimby), diagnosis and treatment (Lloyd E. Craver), and hormones and cancer (Howard C. Taylor, Jr.). These are followed by discussions of cancer of special organs—the skin, lips, and tongue (Hayes Martin), the breast (Frank E. Adair), the uterus (Taylor), the stomach (George T. Pack), the rectum, (George E. Brinkley), the bladder and prostate (Benjamin Barringer). Finally, the function and diseases of the thyroid gland (Wm. L. Watson), and trauma and cancer (Ewing) are considered. Section III, by Little, deals with the methods to be used by the Women's Field Army in public education on the subject. A word of special commendation should go to Jean Lorenz for the clear and graphic sketches and diagrams that illustrate the manual.

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The Marihuana Problem in the City of New York. *Sociological, Medical, Psychological and Pharmacological Studies.*

By the Mayor's Committee on Marihuana. The Jaques Cattell Press, Lancaster, Pa. $2.50. xii + 220 pp. 1944.

The Mayor's Committee of New York City, appointed to study the prevalence of marihuana usage in New York, set out to answer the following cogent questions: 1. To what extent is marihuana used? 2. What is the method of retail distribution? 3. What is the general attitude of the marihuana smoker toward society and toward the use of the drug? 4. What is the relationship between marihuana and eroticism? 5. What is the relationship between marihuana and crime? 6. What is the relationship between marihuana and juvenile delinquency? In the opinion of the reviewer, the committee adequately completed its stupendous task and in addition established a volume which will stand as an authoritative treatise on the pharmacology, chemistry, and sociological aspects of this intriguing drug.

The committee reported more than 500 vendors of the drug in New York City. The use was confined almost exclusively to the smoking of cigarettes. The cigarettes were smoked most frequently in company with others in especially decorated incense-laden rooms called "tea-pads." Several hundred of these "tea-pads" were discovered in Harlem. The highest percentage of marihuana smokers was found among the black race. The investigation showed that marihuana smoking did not produce a tolerance for the drug or a true addiction with withdrawal symptoms. The sensations desired by the habitués were a feeling of contentment, inner satisfaction, and a free play of the imagination. The relation between marihuana usage and eroticism was found capricious.

The complete pharmacological and chemotherapeutic studies recorded are commendable. S. Loewe confirmed that the principal site of action of the drug is the brain and that the peripheral effects are negligible. No scientific therapeutic use of marihuana could be established.

John C. Krantz, Jr.

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Bugs and Bullets.

By J. Breckinridge Bayne. Richard R. Smith, New York. $2.75. 256 pp. 1944.

Bayne knows little of literary style, but he has a story of absorbing interest to tell, the story of his own experiences in war-torn and typhus-ridden Roumania during and immediately after the first World War. He is justly proud of his services, for he accomplished wonders under the most adverse conditions, and no little heroism was required. Interspersed with the medical story are many anecdotes of Roumanian life and customs, many descriptions of countryside and people. The book is illustrated from the doctor's own collection of photographs. The central story of ingenious surgery and tireless combat of disease and malnutrition is of double interest in these days when history is repeating itself.

Bentley Glass

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Fundamentals of Bacteriology. *Third Edition.*

By Martin Frobisher. W. B. Saunders Company, Philadelphia and London. $4.00. xvi + 824 pp. 1944.

The third edition of this book is a comprehensive text in the field of general bacteriology, including considerable related material with which the practising bacteriologist must ordinarily work—there are, for example, chapters on pathogenic protozoa and fungi. A new chapter on the pleuropneumonia group of organisms and the introduction of new discussions of aerobiology and the use of aerosols, problems of metabolism, bacteriostasis, electron and fluorescence microscopy, and other subjects of current interest and importance add much to the value of the publication. The treatment of viruses and virus diseases is a great deal more thorough than in the previous edition.

Although the book is written from a primarily medical viewpoint, it does live up to its title, in that such topics as industrial fermentations, vitamin assays, sanitary and soil bacteriology, and plant diseases are well presented. The inclusion of chapter bibliographies extends the usefulness of the text and the illustrations add to its interest as well.

In dealing with a science which has so broad a scope and in which developments are confusingly rapid, the book succeeds in being practical and informative, readable, concise and up-to-date.

Harriette Vera

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Japan's Secret Weapon.

By Barclay Moon Newman. Current Publishing Company, New York. $2.50. 223 pp. 1944.

Pestilence, whether or not it is Japan's secret weapon, has certainly played a dominant role in history; it still does and will continue to do so. There is some evidence that the Nipponese have waged bacterial warfare, at least experimentally, using plague bacilli as a weapon against China. It is not, however, necessary to assume that the Philippines were captured because the Japanese took malaria there. Epidemiologists have long known that the introduction of a new population into an area tends to make them more susceptible than the native people to indigenous infections, and that malaria has been firmly established in the South Pacific for some time.

Professor Doctor Yoneji Miyagawa of the Tokyo Imperial University is said to be the diabolical inventor and director of the mass-murder program. Meanwhile, Americans have been in the throes of sleeping sickness, as evidenced by the Pearl Harbor attack and tuberculosis in New York. Contrary to Newman's opinion, scientists could hardly have been unaware of the possibilities of bacteriological warfare. Perhaps a better term would be microbiological warfare to include the various small pathogenic agents, both plant and animal, with which the "benevolent" Miyagawa is concerned.

The theses which the author presents—the possibilities and potentialities of warfare with microbes and the comparative lethargy of the American citizenry and their government in regard to their own health problems — are well founded. It is most unfortunate that the timely presentation of this material is not more logical and realistic. Emotional exaggerations and reiterations of subject matter, with excessive and poorly supported claims, tend to be unconvincing. The power of plagues needs no garnishing. In the public schools, in the press and in ordinary conversation, people customarily use rather more scientific terms without referring to disease-producing organisms as rodlets or cocktails. A more solemn, respectful, and vigorous reminder might have made a more forceful warning.

HARRIETTE VERA

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THE MICROBE MAN: *A Life of Pasteur for Children. Puffin Story Books.*

By Eleanor Doorly, with an introduction by Professor Pasteur Vallery-Radot. Penguin Books, Harmondsworth, Middlesex; New York. 9d. (paper). 112 pp. 1943.

In simple and moving language Miss Doorly has told for children the story of Pasteur, basing her account chiefly upon Vallery-Radot's biography. This is a book for all biologists to read to their children between the ages of eight and fourteen. It is a worthy introduction to the spirit of science.

◆

THE BABY MANUAL. *A Practical Guide from Early Pregnancy through the Second Year of Life.*

By Herman N. Bundesen. Foreword by Thomas Parran. Simon and Schuster, New York. $3.00. xii + 590 pp. 1944.

Over 10,000,000 copies of the original form of this manual have been distributed. In its more extensive new version and fresh format it should be useful to many additional parents. It is simple in style and includes answers to virtually every question about baby care that even the most ignorant mother could think of asking. Its most excellent feature is its organization, which makes it possible to find desired information easily and quickly. The first two parts of the book deal respectively with prenatal care and care of the baby (feeding, clothing, bathing, sleep, fresh air, sunshine, sickness, training). The second half is in question-and-answer form, arranged according to the infant's age, beginning with the premature baby, proceeding month by month up to the age of one year, and then through the second year in periods of three, three, and six months.

◆

YOU ARE YOUNGER THAN YOU THINK.

By Martin Gumpert. Duell, Sloan and Pearce, New York. $2.75. ix + 244 pp. 1944.

The author, an exile from Germany who is now an American citizen, discusses in remarkably clear, simple, and forthright style the problems of aging. Only for those who are not looking forward to, or dreading, the years of old age, or who have no concern for maintaining their health and vigor through the years will this book have no interest. The first part of the book is a general account of the biology of aging, of normal old age, and of the social problems of aging. The second part, an overgrown appendix as large as the body of the book, is slightly more technical, taking up the diseases of old age organ by organ, from the skin to mental disturbances. This portion will be a useful handbook for consultation as ailments develop.

The book opens with an amusing account of the founding and successful efforts of the Committee on Longevity of the class of 1900 of the College of Physicians and Surgeons of Columbia University to keep the members of their group alive and in health. Then the life-span and the ratio between age groups in the population, the connection between age and disease, longevity, the changes of aging, and physiological age and biological time are discussed. Emphasis is laid on the importance of energy-saving and of keeping up physical and mental activity. Gumpert also considers the effects of the weather, diet, stimulants, and sex activities on older persons. The account of Bogomolets' work in Russia with the antireticular cytotoxic serum (ACS) in cancer treatment, bone fracture, and rejuvenation is arresting and leads to the hope that it may soon be confirmed in this country. The author supports the philosophy of a creative old age with an abundance of instances. Altogether, he has written one of the best recent books on scientific subjects for the general public. Biologists will find it well worth their attention.

BENTLEY GLASS

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HOUSING AND HEALTH. *Design for Britain (Second Series), Number 26.*

By Sir John Boyd Orr and Frank Wells. J. M. Dent and Sons, Ltd., London. 6d. (paper). 31 pp. 1944.

This is one of a series of pamphlets issued recently in Britain by the Cooperative Permanent Housing Society, and designed to stimulate thought on post-war reconstruction.

It begins with a plain statement of facts and figures on the relation between housing conditions and delinquency, the death rate, and the incidence of diseases. On the basis of further facts regarding the extent of housing requirements, a strong plea is made for giving absolute priority in labor and materials to the post-war housing program.

In order to plan housing for health it is necessary to have a master-plan—to estimate the future development of industries, to determine their location, and to build new towns or rebuild old towns in relation to industrial needs. The authors advocate postponement of such a master-plan until after the war, when it will be more possible to forecast the industrial future, and when those who have returned from the front will be able to share in the planning. A practical scheme is put forward for providing temporary housing in the interim.

There is much that is controversial in this booklet, and much that is applicable to housing in other countries.

EILEEN SUTTON GERSH

THE HOSPITAL IN MODERN SOCIETY.

Edited by Arthur C. Bachmeyer and Gerhard Hartman. The Commonwealth Fund, New York. $5.00. xiv + 768 pp. 1943.

In this collection of readings the authors have united 145 articles written by 98 authors. These contributions, which have so far been widely dispersed in different journals, actually cover the whole field of hospital science.

The general orientation of the hospital, especially in view of such new problems as hospital service plans, systematic public relations, and social service is discussed extensively. Management and financial control in general, as well as administrative details such as the problem of the trustee, the superintendent, the choice of a medical staff, nursing education, legal problems, and plant maintenance, are abundantly dealt with. Such technical questions as construction, and the handling of special departments (anesthesia, x-ray, obstetrics, laboratories, etc.) are ably explained.

The overwhelming majority of the contributions is extremely valuable and representative. A treatise composed expressly by one or only a few authors would probably have avoided a number of repetitions and rather tiresome generalities, and would have gained in clearness and compactness. On the other hand, it probably could never attain the amazing richness and manysidedness of this handbook, which is due to be a standard work in its field for quite a number of years. Extensive "References for further reading" are another valuable feature of the work. The absence of an index is regrettable.

ERWIN H. ACKERKNECHT

ANIMAL NUTRITION

LA NOVELA DE LAS VITAMINAS.

By Arturo Leon Lopez, with a prologue by Pedro Escudero. Orientacion Integral Humana, Buenos Aires. $12.00m/arg. 449 pp. 1943.

This volume might serve as a script of a movie to be entitled 'Vitamin Fantasia.' Episodes such as 'the vitamin of the motorist,' 'the vitamin of the mariner,' the vitamins of 'the nerves, of youth, of mental equilibrium, of fecundity' follow one another in breathless succession, and indicate the highly popular audience to which this book is addressed. Passing from lyrical realms that invoke Lord Byron, Brillat Savarin, and Escoffier, the dietary tables that recommend two and one-half glasses of milk daily for the adult male reviewer come as somewhat of an anticlimax. Scientific lapses, such as concern, for example, the roles of vitamins C and E, are probably not greater than ordinarily encountered in a volume of this appeal. There is plenty of historical background for the discoveries of the vitamins, in the manner of *Hunger Fighters*. The illustrations for this book are highly original, frankly 'poster art' exhibits, with here and there a hint of Dali; properly reproduced, many could serve as excellent adjuvants for school teaching and adult education. Emphasis has at least been placed on foods rather than vitamin pills. A word of cavil should be directed at the pictures of eminent investigators that adorn the book. They are reproduced so fuzzily that it is doubtful whether their own graduate students could recognize them. In conclusion, one may catch up with one's Spanish and with vitamins (the quintessence of life) by means of this entertaining book.

H. R. CATCHPOLE

INADEQUATE DIETS AND NUTRITIONAL DEFICIENCIES IN THE UNITED STATES: *Their Prevalence and Significance. Bulletin of the National Research Council Numer 109.*

Report of the Committee on Diagnosis and Pathology of Nutritional Deficiencies, Food and Nutrition Board; H. D. Krause, Chairman. National Research Council, Washington. $2.12. ii + 56 pp. 1943.

This bulletin is an excellent report of the Committee on Diagnosis and Pathology of Nutritional Deficiencies of the Food and Nutrition Board. It is a review, bringing together the results of dietary surveys and nutritional appraisal which have been scattered widely in various journals. It also includes some previously unpublished material. Some of the data have been recalculated and reclassified on a uniform, authoritative, and comparable basis.

The first division of the report is titled "The Prevalence of Inadequate Diets as shown by Surveys." This includes a discussion and table of recent standards and systems which have been used in evaluating diets. It contains also the results of surveys conducted in 1938–40 and 1940–43. The surveys were most inclusive, being made on school children and adults in all sections of the United States; on people of various income groups; on people of various races. The results are stated for each survey in percentages of the group failing to meet the daily allowances, and then the results are combined and tabulated in various ways. These are excellently done, since they show comparisons of the various groups tested. Because of the criticism that "the recommended dietary allowances presumably represent 'optimum nutrition,' and perhaps many persons who do not have the margin of safety are in no way deficient," some of the surveys have been incorporated in tables which present the proportions of families whose diets fail to meet not only the full recommended levels for constituent nutrients, but also 75 per cent, 50 per cent, and 25 per cent of these levels. The authors say "from this scale any one can take his choice of levels as a standard." All of the surveys showed the marked prevalence of dietary inadequacies as judged by recommended standards.

The second division of the report is on "Deficiency States: Their Causes, Forms and Detections." This part discusses the point that surveys indicate only dietary deficiencies of a given period. Deficiency states due to cumulative effects are more prevalent and severe than indicated by a dietary survey, for a person's nutritional status depends on the events of all past days. Methods are being made available to detect these states.

The third division is titled "The Prevalence of Deficiency States' and summarizes (1) the recorded prevalence of severe, acute forms as obtained from (a) evidence from official mortality rates, and (b) from hospital admission rates; (2) the recorded prevalence from chemical examinations (this includes tables); (3) medical assessment of nutritional status. All of these indicate that deficiency states are common among the population of the United States.

The fourth division deals with the "Significance of Deficiency States and Optimum Nutrition." This division considers the effects of proper diet on growth and development; the effect of prenatal diet on childbearing; the effect of avitaminosis on well-being and efficiency; diet and dental caries; nutritional status in relation to susceptibility and resistance to infections; and the application of the significance of optimum nutrition.

The final division is the "Summary and Conclusions" and brings most clearly the results of the surveys—that there is a widespread prevalence of moderately deficient diets and that this presents a preventive and corrective problem.

The bulletin also contains a bibliography containing 189 references. The report is one which is excellently written. The results of the surveys are stated clearly and concisely, and sound conclusions are drawn at the end of each division. The final summary and conclusions bring together, briefly, in well chosen statements, the results of these far-reaching surveys.

MARGUERITE M. SCHMIDT

◆

HANDBOOK OF NUTRITION. *A Symposium Prepared Under the Auspices of the Council on Foods and Nutrition of the American Medical Association.*

American Medical Association, Chicago. $2.50. 586 pp. 1943.

This excellent Symposium consists of an introduction by James S. McLester, chairman of the council, and twenty-four articles on various phases of nutrition, each article written by an authority in the field, as follows: Proteins in Nutrition, Howard B. Lewis; Role of Fat in the Diet, W. R. Bloor; Calories in Medical Practice, E. F. DuBois and W. H. Chambers; Water and Salt Requirements in Health and Disease, John H. Talbott; Principal Mineral Elements in Nutrition, I. G. Macy; Iron in Nutrition, C. W. Heath; Iodine in Nutrition, G. M. Curtis and M. B. Fertman; The Trace Elements in Nutrition, M. E. Shils and E. V. McCollum; The Fat Soluble Vitamins, Hugh R. Butt; The Water Soluble Vitamins, C. A. Elvehjem; Foods of Plant Origin, Leonard A. Maynard; Foods of Animal Origin, H. C. Sherman; Unusual Foods of High Nutritive Value, Russell M. Wilder and Thomas E. Keys; The Preservation of the Nutritive Value of Foods in Processing, Edward F. Kohman; Improving the Quality of Cheap Staple Foods, George R. Cowgill; Recommended Dietary Allowances, Food and Nutrition Board, National Research Council; The Feeding of Healthy Infants and Children, Philip C. Jeans; Feeding the Aged, Edward L. Tuohy; Nutritive Requirements in Pregnancy and Lactation, J. Harry Ebbs; Adequacy of American Diets, Hazel K. Stiebeling; Medical Evaluation of Nutritional Status, H. D. Kruse; Nutrition in Preventive Medicine, W. H. Sebrell; Conditional Malnutrition, Norman Jolliffe; Principles of Diet in the Treatment of Disease, Tom D. Spies. Each of these articles is a review of the latest literature in the field, and contains the references to the original literature at the bottom of each page. On the whole, the papers are clear, concise and to the point, covering the available information.

While space does not permit comment on all of the papers included in this handbook, a few may be given special comment: The article on proteins is a fine review of the subject, including a brief discussion of the structure, value of amino acids, dietary needs, and recent developments in protein metabolism. Butt, in his paper on "The Fat Soluble Vitamins," has given "data which it is hoped will be of value in orienting conceptions in a rapidly changing subject." The subject of the water-soluble vitamins is well summarized by Elvehjem, who includes a general summary of the more significant facts and stresses the nutritional aspects of these vitamins. Talbott has a fine review of the water and salt requirements in health and disease.

At the front of the book is a list of the contributors, giving the places with which each of them is associated. There is an excellent index. The book will be a very valuable one for anyone interested in the field, and is highly recommended.

MARGUERITE M. SCHMIDT

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THE ORIGIN OF FOOD HABITS.

By H. D. Renner. Faber and Faber Ltd., London. 15s. 261 pp. 1944.

It has been increasingly realized that food habits are neither the expression of our unswerving instincts for caloric and vitamin requirements nor simply the unpredictable product of innate foolishness, as they first appeared to somewhat naive and bewildered dietitians. The book under review is one of the most interesting attempts to find new ways of understanding food habits. The approach of the author is "psychological," a term whereby he comprises two entirely different sets of motivations under a common label, namely, reactions toward food dictated by the physiology of our senses; and true mental reactions, often entirely illogical and irrational, and understandable only upon historic grounds. While the latter have found larger attention in the recent past, to emphasize the former is a particular merit of the author. That some of his physiological explanations are highly controversial and probably rationalizations of the irrational, does not detract in the least from his merits, and is unavoidable in view of the fragmentary character of our knowledge of the physiology of our senses.

The author reviews in detail the influence of climate and of original techniques in agriculture and food preservation on the formation of food habits, especially in the British Isles, as well as the changes brought about by modern manufacture and global economy.

An extraordinary wealth of data and of ideas are handled competently in this small book. Their very overflow has produced a staccato style which does not always make good reading. This minor weakness will not deter those interested from studying what is one of the most important publications in the field of food habits.

Erwin H. Ackerknecht

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All About Feeding Children.
By Milton J. E. Senn and Phyllis Krafft Newill. Doubleday, Doran and Company, Garden City, New York. $2.50. xviii + 269 pp. 1944.

Here is a handbook on children's nutrition that is compact, well organized, and different. The first section of the book takes up needs and problems of children's nutrition according to the child's age, paying attention not only to what should be fed and how it should be prepared, but also to the importance of psychological factors. The second section is a new sort of cookbook, detailing many methods of preparing the main types of foods so as to make them appetizing to children. Parties and picnics are not forgotten, and the novel chapters on the school lunch box, on traveling with young children, and on food and the war complete an exceptionally sound and helpful book for the home. It should also be useful to dietitians in schools, hospitals, and other children's institutions.

Nutrition and National Health *being The Cantor Lectures delivered before The Royal Society of Arts 1936.*
By Major-General Sir Robert McCarrison. Faber and Faber Limited, London. 6s. 75 pp.; 3 plates. 1944.

A reprint of three lectures delivered in 1936, this little book still provides a fundamentally sound outline of the principles of nutrition, though in a few respects it is not quite up to date (vitamin K, for instance, is not mentioned). The material is excellently presented, and it may be recommended to the general reader and to those who are concerned with nutrition in its social applications.

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BIOCHEMISTRY

Advances in Protein Chemistry. *Volume I.*
Edited by M. L. Anson and John T. Edsall. Academic Press, Inc., New York. $5.50. xi + 341 pp. 1944.

At first thought, it may seem peculiar for this kind of book to be reviewed by a histologist. Actually, the book is very stimulating to the reviewer, and should be so to morphologists generally. There are numerous indications that biochemistry and histology are coming to the point where things as seen (with the white light, ultraviolet, or electron microscopes) are to be characterized in physical and chemical terms; that is, when quantitative chemically-valid terms will be used to describe structures. This merging of the two fields is bound to catalyze cytology, for it exposes enormous possibilities for the functional interpretation of morphologic elements. These comments apply particularly to five of the eight articles included in the volume (Chargaff, "Lipoproteins"; Schmitt, "Structural Proteins of Cells and Tissues"; Greenberg, "The Interaction between the Alkali Earth Cations, Particularly Calcium and Proteins"; Greenstein, "Nucleoproteins"; Bailey, "The Proteins of Skeletal Muscle"). The remaining articles are by Treffers, "Some Contributions of Immunology to the Study of Proteins; Chow, "The Purification and Properties of Certain Protein Hormones"; and Payne and Stuart, "Soybean Protein in Human Nutrition."

Each article is accompanied by an extensive bibliography. The author and subject indices covering all articles are helpful. It is regrettable that the binding, paper, and printing are not of as high quality as the contents, because of the government's regulations for conserving paper and other materials.

I. Gersh

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Laboratory Experiments in Biological Chemistry.
By James B. Sumner and G. Fred Somers. Academic Press, Inc., New York. $2.60. vi + 169 pp. 1944.

This laboratory manual has been prepared by the authors for use in their own courses, but it should be of value to many who are looking for a laboratory manual "ready to use."

The first pages of the manual contain "General Instructions." These are excellent ones for any course. They deal with "safety first regulations," "cleaning solutions," "concentration of solutions," and "preliminary training in analytical chemistry." The instructions are clearly written and very easily understood.

The manual is divided into two parts, each part for one term's work. In the first part, the experiments are grouped under the following headings: lipids; bile; acetone bodies; formaldehyde and methyl alcohol; dialysis; carbohydrates; plant pigments; determination of Vitamin C; gastric analysis; urinanalysis; blood-quantitative analysis; and electrometric determination of pH. Part II experiments are under the following headings: amino acids; proteins; hemin, hemoglobin, and related compounds; agglutination; enzymes-general, enzymes-preparation; activity determination; and alcoholic fermentation.

The experiments that have been chosen as representative ones under each of these groups are good ones. They are clearly written and most explicit. Much explanation of the reactions involved, of the precautions necessary, and of the errors that might occur are included. Questions are asked. Directions for the preparation of various solutions are given,—an excellent feature, since the student is given this information directly Original literature references are made at many points.

The order of the experiments is an unusual one, but this is a minor criticism, since the order of performance of the experiments can be determined at will. The number of quantitative urine experiments is quite small. It is true that the authors have said in their preface that they have chosen "typical" ones. However, it is customary in most biochemistry courses to do a quantitative analysis of a 24-hour sample, and the directions for such an analysis are lacking in this manual. The number of experiments on enzymes is quite large for the average course in biochemistry. However, on a whole, the manual is an excellent one that could be readily adapted to any class.

MARGUERITE M. SCHMIDT

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THE CHEMISTRY AND PHARMACY OF VEGETABLE DRUGS *Dealing with the Derivation and Properties of All the Principal Vegetable Drugs.*

By Noel L. Allport. Chemical Publishing Company, Inc., Brooklyn. $4.75. viii + 252 pp. 1944.

This treatise includes chemical, pharmaceutical, and pharmacognostic descriptions of many vegetable drugs. The author has not limited the scope of the text to the drugs recognized in the official compendia, but includes many roots, leaves, and barks that are no longer official.

The division of the subject matter is based upon the character of the drugs discussed. Thus several chapters deal with alkaloid-bearing drugs such as opium, belladonna, and cinchona. Other chapters are concerned with resinous drugs like jalap and podophyllum and senna, and other cathartics find their appropriate places in other chapters.

Each drug is introduced historically. Its pharmacognostic characters are outlined and often completely illustrated. The constituents of the plant are treated at length, with special emphasis on those which have medicinal value. The chemistry of the alkaloidal substances is included. Galenical preparations made from the crude drug or its active principles are described. The standardization of the various vegetable drugs is given in great detail, except when the assay is biological in character. In these instances the author gives only a brief outline.

The style of the author is lucid, and as one peruses the volume he reaches the conclusion that the book is an expression of the author's experience with the drugs which he discusses. Indeed, this volume is an excellent reference and guide to the pharmacist, drug control chemist, and pharmaceutical manufacturer.

JOHN C. KRANTZ, JR.

PSYCHOLOGY AND ANIMAL BEHAVIOR

THE PHYSICAL BASIS OF PERSONALITY. *Pelican Books. By V. H. Mottram. Penguin Books, Harmondsworth, Middlesex; New York.* 9d (paper). 126 pp. 1944.

In this book a description of meiosis is accompanied by the footnote: "This account, in fashion when the writer was a student, is no longer held to be true . . . ". Says Mottram: "No one would deny that sex conditions personality," and after some discussion of the justification for generalizations about sex and personality, " . . . justification or not, it hardly matters so long as there is a general agreement, which I think is undoubted, that sex conditions personality." Whereupon he presents the argument that sex (and therefore personality also) is determined by the chromosomes. "This," he writes later, "is the first and ineluctable piece of evidence that our personalities are determined by our chromosomes."

Before one looks for further evidence in his discussion of the nervous system and endocrines, one may wonder at this point why Motram was impelled to write a book on this subject, unless one has read the warning preface: "The chasm between the opposing points of view [of science and religion] must be bridged."

For more than three quarters of the book the writer plays devil's advocate for a materialist outlook—our personalities are determined by our chromosomes and these in turn are subject to fixed laws of behavior and probability—this is all there is to it. He rejects various attempts to escape from this position through philosophical argument, and finally chooses to escape by counterposing the experience of the mystic to that of the scientist—the genes determine only the "persona," the character portrayed upon the stage. The true self of the actor cannot be apprehended by the scientist as such, but only by the mystic.

Eileen Sutton Gersh

◆

The Psychology of Women. *A Psychoanalytic Interpretation. Volume One.*

By Helene Deutsch. Foreword by Stanley Cobb. Grune and Stratton, New York. $4.50. xiv + 399 pp. 1944.

In this volume Helene Deutsch has brought together results of a continuing interest in what Freud referred to as "the problem of woman." Freud didn't expect woman to solve her own problem because, as he said, "You are the riddle yourselves." If he were living, he might very well confess that in this book Helene Deutsch has gone a long way to explain to many people's satisfaction many aspects of feminine psychology.

Using the psychoanalytic method, which essentially is based on the theory that the psychologic structure of the person is formed in the early years, she divides the book into three essential parts. The first deals with the young girl's psychologic development into womanhood, a process beginning in the early years and extending through puberty, in the course of which "the feminine core" is definitely formed. There are chapters on prepuberty, early puberty, puberty and adolescence, and menstruation. The second part deals with the detailed examination of this feminine core. Deutsch finds that there are three essential traits of femininity: narcissism, passivity, and masochism. Accordingly there are chapters on eroticism: the feminine woman, in which are described three types of the feminine woman; feminine passivity; and feminine masochism. In the third part certain types of women who do not appear on the surface to fit into the three feminine types are described. Accordingly there are chapters on the "active" woman; the masculinity complex; and on homosexuality. Finally there is a chapter on the influence of the environment on feminine psychology. The book ends with a bibliography and index.

It is impossible to give in detail the gist of the observations and theories exposed in this book. The author draws on a vast experience in dealing with girls and women of all ages, and because of the wealth of her material what she has to say carries the ring of authenticity. This reviewer is less impressed with her use of material from belles-lettres. It may or may not be true, as she insists, that such material, while less objective, is "all the more true because more inspired." It is quite possible that the author has taken too literally to heart her own deduction concerning woman, that her strong point is intuition, not logical reasoning. This reviewer, being a male, would have preferred that she stick to clinical material. To build up a theory and then to argue its worth on the basis of a mythical construction from someone's imagination does violence to my scientific training. The mythical construction might be all she says it is; again it might not. By contrast she makes very telling use of hospital records, and, it may be noted, not her records, but records taken by other people and used for all they were worth to illustrate her points.

Speaking generally, Deutsch would say that women are different psychologically from men in their greater capacity for emotion, in their use of emotion, and, perhaps related to this, in their use of intuition to arrive at understanding rather than by cold logical reasoning. In fact, she feels that really feminine women do not approach men in their intellectual processes, but are vastly superior in their empathic potentialities.

Here and there through the text she has deviated slightly from the true Freudian doctrine, and these deviations seem well supported by her own observations, but for the most part she follows strictly Freudian doctrine, including penis envy as a fundamental of all womankind. She says this is so regularly found in analysis that it may be assumed as the universal phenomenon. This is one of the points where a traditional but enlightened psychiatrist would question whether the reputed universality of the findings is as much the consequence of the use of analytic method as of the intrusion of analytic dogma into the findings.

Deutsch concludes that women are by nature monogamous, but there must be better reasons for concluding this than some she advances. For instance, she alludes to the distress of a girl over the questionable fatherhood of her child. This child was born in a country where the fatherhood of the child is said to be of no social consequence, but the author glides over the fact that her contact with the girl was in a country where such a state of affairs obviously did not exist. How much the girl's distress was due to environmental factors is not stated. Was intuition at work in the author here?

It is, however, not the wish of this reviewer to carp at a few things which rub him the wrong way. The volume obviously is full of factual information which anyone would be glad to possess.

The author promises a second book having to do with "the central problem of feminity—motherhood." The first volume therefore deals with the development of the individual woman's personality, and the second volume will deal with her as a servant of the species. If the second volume is as provocative of thought as this one, then the author will have furnished an important and well rounded contribution toward a matter of importance to all psychiatrists, to say the least, and conceivably to all women and men.

WENDELL MUNCIE

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RORSCHACH'S TEST. *I. Basic Processes.*

By Samuel J. Beck. Foreword by Willard L. Valentine. Grune and Stratton, New York. $3.50. xiii + 223 pp. 1944.

In this book Beck demonstrates exactly how to go about the evaluation of the Rorschach test responses by the use of a few examples examined in detail. He follows very closely Rorschach's original work, adopting the English symbols used in the Lemkau-Kronenberg translation of "Psychodiagnostik." The book will be found very useful to Rorschach testers.

WENDELL MUNCIE

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SOCIAL PSYCHOLOGY. *Second Edition.*

By Kimball Young. F. S. Crofts and Company, Inc., New York. $4.00. viii + 578 pp. 1944.

Those who are acquainted with the scholarship, thoroughness, and readability of the first edition of Young's *Social Psychology* will welcome this new edition, equally interesting and stimulating, with some chapters expanded and others wholly new.

The pre-human sources of social interaction, in the social life of lower animals, especially monkeys and apes, are presented in the second chapter. The next, on Culture and Personality, includes a six-page comparison, in columns, of the principal cultural factors of eight selected native peoples, and a three-page comparison of such features of Japanese, Germans, and Americans. Two chapters deal with the elements and mechanisms entering into the rise of the social self, with a clear and appreciative exposition of George H. Mead's theory of the "I" and the "Me," an elaboration upon the concepts of William James, Josiah Royce, J. M. Baldwin, and Charles H. Cooley. The treatment of social cultural reality has been extended. In trying to meet the needs of a better understanding of past and present national psychology, the author has added one chapter on the psychology of revolution and two on war and wartime morale. The importance of the motion picture and of radio have received increased attention, in the treatment of public opinion. Two chapters are devoted to propaganda, with special attention to the two World Wars; and, finally, the nature and the use of power are discussed as pertinent to the revolutionary threat to democratic culture and the facts of total war.

The format is good; the style is clear, easy, and attractive. Suggestions for further reading are provided for each chapter. An index of names as well as of subjects is given. This edition is entitled to a place among the most popular and valuable textbooks in social psychology.

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WAR NEUROSES IN NORTH AFRICA. *The Tunisian Campaign (January–May 1943).*

By Lt. Col. Roy R. Grinker and Capt. John P. Spiegel. Prepared and distributed for The Air Surgeon Army Air Forces by the Josiah Macy, Jr. Foundation, New York. Paper. 300 pp. 1943.

This book has finally been taken off the restricted list by the Air Surgeon of the Army Air Forces. The authors discuss their experiences with war neuroses in the Tunisian campaign. The book is heavily documented with case records of the following clinical syndromes—free-floating anxiety states, both severe and mild, somatic regressions, psychosomatic visceral disturbances, conversion states, depressed states, concussion states, exhaustion states, psychotic states, and malingering. Furthermore there are chapters on the special psychiatric problems in the Air Forces both among ground and flying personnel, with examination into their etiology from the constitutional standpoint, from the standpoint of previous neurotic trends, of sociological factors, physical state, and psychological factors. There are further chapters on treatment procedures, of which the most interesting, because the newest, is what the authors call narcosynthesis, reliving of the traumatic experience under pentothal sodium narcosis with an active part being played by the physician, who enacts whatever role the drama demands in the interests of a better synthesis of the patient's ego. Psychotherapy, convulsive shock treatment, continuous sleep as well as other standard procedures are also discussed briefly. There is a final chapter on psychodynamics, with topics on factors augmenting anxiety, factors protective against anxiety, conditions breaking down the capacity for handling anxiety, the dynamic struggle of the ego with anxiety, psychobiological mechanisms, the dynamic source of various symptoms of the war neuroses, the dynamic effect of narcosynthesis and psychotherapy, and the reconstructed ego and its vicissitudes.

It is a thrilling experience to read this book, and one is grateful to the authors for presenting the material so forcefully. The various reaction types have been described in numerous papers from the British Isles as well as by the military service of the U. S. Army and Navy, and there may be nothing new in these descriptions, but at least the descriptions are wonderfully done. There are only a few comments which the reviewer as a civilian psychiatrist would feel prompted to make. In the first place, the book has a distinctly psychoanalytic flavor, as is to be expected from its authorship. This bias goes a little far perhaps when, for example, in the course of discussing a patient with hysterical conversion manifestations the authors state, "The libidinal component in the hysterical conversion states could not be determined by us in the time available. The all pervading reality of the war situation so dominates the clinical picture that unconscious erotic factors are difficult to discern." (p. 59). The implicit assumption here is that the hysterical conversion states must have a libidinal component, and that there is no other proper final explanation of these states. This may or may not be true despite analytic dogma. Likewise, "Severe conflict over hostility is indicative of chronic neurosis." (p. 146). It is certainly true that a great many chronic neurotics display much hostility, as the authors go on to state, but that this is an indication of chronic neurosis remains to be proven.

Especially interesting was the confusion (not of the authors apparently) in the original diagnosis of certain states of acute and severe free-floating anxiety with schizophrenia. These several cases described by the authors came to them with an initial diagnosis of schizophrenia. The authors state, "It is our opinion, however, that prior to the institution of therapy, this condition (severe anxiety) may be distinguished from schizophrenia by the quantity of anxiety exhibited by the patient." Also, "Differential diagnosis from schizophrenia often can only be made by a therapeutic test with intravenous sodium amytal or sodium pentothal, to which the anxiety states respond promptly and dramatically." To this reviewer there is a certain underlying inadequacy in this attitude toward differential diagnosis. Plainly these patients were in panic, and panic has very much the same character as delirium, in the sense that when present it is apt to cover over the underlying personality so completely that it is impossible to state whether one is seeing panic in a formerly and basically well adjusted person or panic in a person with a disrupted personality. We were always taught that when panic is present it is best simply to make that diagnosis and wait for the further eventualities to see what underlies the panic. The use of sodium pentothal as a differential diagnostic feature, however, is important in this situation and corresponds roughly with the massive sedation used in civilian panic states, out of which any kind of personality may emerge. It is no tribute to the teaching of psychiatry in this country that this fundamental fact should be so misunderstood.

The authors are at their best and most dramatic in describing their success with narcosynthesis. This evidently has been a very valuable therapeutic agent, and by its use has thrown a great deal of light on the actual mechanisms involved in the production of war neuroses and in their alleviation. For this, if for nothing else, every practicing psychiatrist could be grateful to the authors.

Wendell Muncie

The War and Mental Health in England.

By James M. Mackintosh. The Commonwealth Fund, New York. 85 cents. 91 pp. 1944.

The author has given a very lucid account of the problems of mental health in Great Britain. The book is divided into two parts—Part I, The Impact of War, and Part II, Mobilization for Peace. In Part I the reader is taken through the process of adjustment in going from peace to wartime status, through the "lonely year 1940–41," through preparations for the final blows, and "the end of the beginning, 1942–43." Material of this same sort has appeared in various accounts from overseas. Particularly interesting is the story of the evacuation of the children and the problems raised by this procedure, problems which will not end with the coming of peace. Interesting also is the boost to the general morale with the declaration of war, the inability of the common people to accept defeat, and the dogged persistence of preparation for the final onslaught. The author touches rather guardedly and lightly on the problems raised by the American use of England as an advanced base.

In Part II Mackintosh discusses the hospital services, the voluntary organizations for mental health, professional education in mental health, and some problems of the future. Already a great deal has been accomplished in Britain in these years through the military and civilian governmental organizations in rehabilitation, but the author looks forward to something better than rehabilitation. He looks forward to professional and lay education in the abundant use of assets in the maintenance of mental health and the prevention of mental breakdown. He envisages, for example, the establishment of preventive health institutions in which there will be basic training, including basic training in mental health with an opportunity for specialization later on, courses open to physicians and to nurses.

Altogether, this is a stimulating book interspersed with humorous bits, and even the story of the most trying years is not a lugubrious thing.

Wendell Muncie

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Military Psychology.

By Norman C. Meier. Foreword by Lieutenant General Ben Lear. Harper and Brothers, New York and London. $3.00. xx + 395 pp. 1944.

This book is an excellent presentation of military psychology divided into Part I—General Principles and Practices, and Part II, Applications and Problems. A full and adequate glossary of 13 pages concludes Part II. One may think of the eight chapters as falling into four groups: A. Social Psychology: Group Conflict, Combat Psychology, Preparation for Morale Combat; B. Educational: Adaptation of Skills to Military Needs, and Learning Military Skills; C. Leadership: Leadership and Coordination, Leadership in Combat Situations; D. Abnormal and Adjustment Psychology: Adjustment to Combat Conditions and Stress.

The author does not give us arm-chair, theoretical psychology but principles and practices based on research and investigation in social psychology, the psychology of World War I and World War II, the psychology of skills and abilities, perception and deception (camouflage), learning, forgetting, teaching and study, and medical and abnormal psychology. The author has not only placed important facts and principles at the disposal of the military forces, but has made available to teachers, public servants, and lay readers many interesting and useful facts concerning the various phases of military psychology, personnel, morale, camouflage, and preventive and remedial mental hygiene.

The style is clear, interesting, attractive. The book is highly informing. All who have relatives and friends in the war will find this a valuable book, one which will help them to appreciate the psychological factors with which military officials, servicemen, psychologists, psychiatrists, and civilians have to deal during the remainder of this war and in many ways after the war. And, it goes without saying, the book is the outstanding textbook on military psychology, being very highly recommended by Lieutenant General Ben Lear of the United States Army.

In Part II there are applications and problems for each of the chapters in Part I. There are also four appendices: A. Suggestions for Handling Interviews; B. Requirements for Miscellaneous Services; C. A Rating Scale for Candidates for Officers Training Schools; and D. Proposed Additional Methods for Selection of Combat Officers. The glossary follows these divisions. There is also an index.

C. Hart Westbrook

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Normal Lives for the Disabled.

By Edna Yost in collaboration with Lillian M. Gilbreth. The Macmillan Company, New York. $2.50. x + 298 pp. 1944.

This is an enlightening, human, inspiring book. The facts and techniques needed by the handicapped are well, fully, and clearly presented. But the philosophy of how to take misfortune and to convert it into an asset, of how to achieve a happy and useful life when the world may seem to have crashed about one, is even more valuable to the reader than the well chosen details of how to prepare for a job and to find and hold it.

The style is direct—the writer speaks directly to the reader; and if he has any human feeling at all, the reader will find the book engaging. Not only the physically handicapped veterans and civilians, but thousands of other men and women who are mentally and emotionally broken as a result of long and inhumane internments will find inspiration and help as they travel the long way back to normal health (if that be possible) and to a satisfying and useful place in the economic and vocational life in the homeland.

The employers of all such handicapped persons, the relatives and friends who wish to help them but find it too difficult a task, teachers, social workers, and mental hygenists—and others, too—will find this presentation a valuable guide in their relationship with returning veterans and civilians from the warring countries of the world.

The treatment is a factual one enriched by the wide and specialized knowledge and experience of the author and her collaborator, both of whom are well known to those acquainted with human engineering in this country.

C. Hart Westbrook

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Psychoanalysis Today.

Edited by Sandor Lorand. International University Press, New York. $6.00. xvi + 404 pp. 1944.

This is a compendium at the hands of twenty-nine different contributors concerning various aspects of psychoanalysis as it stands today. The list of contributions is as follows: Freud's influence on medicine, psychoanalysis and internal medicine, psychosomatic medicine, therapeutic approach to psychosomatic problems, child analysis, the early development of conscience in the child, child-parent relationship, prevention of mental disease in childhood, juvenile delinquency, psychoanalytic social work, mental hygiene, development of the ego-psychology, dream mechanisms and interpretations, sexuality and its role in the neuroses, hysterias and phobias, obsessional neuroses, character formation, pathological character formation, war neurosis, neuroses and psychoses, manic-depressive psychoses, schizophrenias, organic psychoses, the technique of psychosomatic therapy, psychotherapy and psychoanalysis, the psychology of religion, psychoanalysis and sociology, problems of crime, approaches to art, psychoanalysis and literature, psychoanalysis and anthropology. The chapters are short, from ten to fifteen pages, and give a bird's-eye view of each of the topics mentioned above. As with any compendium, the contributions range from the most conservative, sound, and sane to those exhibiting a considerable uninhibited enthusiasm, to say the least. As an example of the former there is Monroe A. Meyer's "Dream Mechanisms and Interpretations," a paper which came out some time ago but which has been included because of its fundamental importance. As a minor example of the latter there is the example given by English in "Therapeutic Approach to Psychosomatic Problems" of the dynamic aspects of anorexia nervosa. English asserts that in this condition the dynamics will finally show that the patient is afraid to eat because she is afraid of becoming pregnant, or that by refusing food she is refusing love or sexuality, and that she actually wants to bite her mother's breasts or father's penis. English's suggestion that the physician must either carry through with the patient as best he may the matter of such dynamics, or be reduced to vitamine and iron injection, seems to leave out of account a middle course where one works with what the patient offers, with the intention of increasing the area of common interest and understanding without the intrusion of special interpretation. If it ends up with such a formulation, all right. If it doesn't (and such patients do get well without such interpretations), this ought to be allowable, too.

Where were Menninger, Rado, Horney, Kubie, and others when the assignments were made?

WENDELL MUNCIE

FREUD'S CONTRIBUTION TO PSYCHIATRY.

By A. A. Brill. W. W. Norton and Company, New York. $2.75. 244 pp. 1944.

Brill, who was directly responsible for the introduction of Freud's work and teachings into this country and who has been an active and revered figure in the psychoanalytic movement ever since its inception here, gives in this book a very dramatic and personal account of Freud's discoveries, his methods of work, and his wide-flung interests. No one will deny the enrichment that has come to psychiatry, to psychology, anthropology, and religious thought through Freud's teachings, and even the lay reader would get from Brill's presentation an easily understandable and telling account. The book is liberally sprinkled with references to Brill which are not in the least annoying, since Brill's warm, democratic, and humorous, although serious nature stands out always. As an epitome of Freud's work this reviewer has read none better.

WENDELL MUNCIE

HUMAN BIOLOGY

ENOUGH AND TO SPARE: *Mother Earth Can Nourish Every Man in Freedom.*

By Kirtley F. Mather. Harper and Brothers, New York; London. $2.00. 186 pp. 1944.

In this small book Harvard's eminent geologist takes a broad look at the problems of human subsistence and finds the fundamental facts grounds for considerable long-range optimism. This does not mean that there is not a "critical question" facing the present century; but Mather is confident that the question is not that bogey of exhausted resources and teeming populations commonly reared. The real issue is whether or not man will have the intelligence to recognize the interdependence of nations and to organize the use of resources on a world-wide scale; whether or not he will find the courage to control not only waste and spoliation but to tackle the problems of population growth with insight and resolution.

This rebuttal of neo-Malthusianism makes out a good case for the abundance of resources (enough of those non-renewable to last 1000 years) for an eventual world population of 28 to 32 hundred millions. The latter figure is based on the assumptions that present population trends will continue and that in yellow, brown, and black peoples they will have the same general character as in whites, though delayed some decades. If we accept these assumptions, the main conclusion follows,—although one may have an uneasy feeling that the author has played down the problem of diminishing returns for labor expended, both in agriculture and in the use of mineral resources, as the richer lands are occupied and the richer stores of ore and fuel are exhausted. Here the hand of science must find a way.

Mather dismisses long-range Malthusianism as an unreal specter, but there is still the very real dilemma that faces mankind in the immediate future in many parts of the world. It is doubtful, according to Warren Thompson, whether in China and India, for example, any significant decline in the birthrate is to be expected for half a century. With a declining death rate already evident, an enormous increase in population is to be expected in the remainder of the present century, barring Malthusian elimination or emigration. To anyone who knows China the view that the Chinese will be able to "find their own salvation by more intelligent adjustments of their own cultures to their resources" (Mather, *Science*, 101:199) will seem over-optimistic. Changing the fundamental culture pattern of an Asiatic people will take considerably longer than will the rapid increase of population. Resistance to methods of birth control on account of religion and outlook, and the ignorance and poverty of the masses that militate against their effective use are well-nigh insurmountable. Mather realizes all this, but his emphasis on long-range, world-wide aspects of the problem tends to minimize them.

The second half of the book is devoted to the consideration of the "critical question." Can activities be coordinated internationally? Should we take the alternative of regimentation or that of democracy? Mather's answer is unequivocally in favor of the latter, which he maintains is more efficient as well as more in accord with human nature. A slight weakness in his argument at this point is that he makes frequent comparisons between the totalitarian countries—Germany, Italy, Japan—and the democracies, especially the United States, but ignores the position of regimented Russia or of the futile pre-war democracy of France.

If it is true that "today the intellectual resources of the totalitarian nations are distinctly inferior to those of the democracies. Mental ability has deteriorated seriously under regimentation," where, as a friend of Russia, does he place the U. S. S. R.?

In the main, this portion of the book presents views that parallel to a remarkable degree those of Julian Huxley recently set forth in *On Living in a Revolution* and elsewhere. "The revolution of our times involves the transition from intellectual anarchy to international order and the advance from an uncontrolled, competitive economy to a regulated co-operative economy"—is certainly as characteristic of Huxley's analysis as of Mather's.

Mather's style is forceful, clear, and readable; his subject is one to which all Americans should give attention. It is not the intention of this reviewer to carp, for, if the book's black is so very black and its white so very white, it is nevertheless a most stimulating analysis. No reviewer could dismiss it with a scant mention.

BENTLEY GLASS

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THE BRUSH FOUNDATION STUDY OF CHILD GROWTH AND DEVELOPMENT II. PHYSICAL GROWTH AND DEVELOPMENT. *Monographs of the Society for Research in Child Development, Volume IX, Number 1. (Serial No. 37).*

By Katherine Simmons. Society for Research in Child Development, National Research Council, Washington. $1.50 (paper). xvii + 87 pp. 1944.

Over a period of many years the late Prof. T. W. Todd organized and directed intensive studies on the normal physical growth and development of children. The present monograph is one of the results of these broad investigations. It deals chiefly with the anthropometric data collected on 999 white children in Cleveland whose parents are of North European ancestry and of above-average economic level. The examinations of these children were undertaken at frequent and regular intervals from birth to 17 years. The data which have here been analyzed statistically approach closely to the best that can be desired, and hence this report contributes unusually reliable cross-sectional age-sex constants for 25 anthropometric dimensions and for assessments of skeletal age during the entire period of active growth. All the many detailed findings are clearly discussed in the text and fully shown by means of tables and graphs. Of the conclusions, the following might specially interest all those with faith in popular age-height-weight charts: "The 'normal' weights found in height-weight-age tables approximate the truly normal only when height is not composed excessively of either leg length or trunk length and when ratings of body breadth are in harmony with ratings of body length."

ADOLPH H. SCHULTZ

WOMEN AND MEN.

By Amram Scheinfeld. Harcourt, Brace and Company, New York. $3.50. xx + 453 pp. 1944.

In spite of its lurid dust jacket, this is a sound, well balanced treatment of the subject of sex differences. The author has written a better book than *You and Heredity*, for while his former best seller was accurate and original, this one adds a thorough documentation of source material, and its style, while still breezy, avoids the charge of sensationalism. It is annoying, however, to find Nature personified throughout.

As a synthesis of genetic, anthropological, and sociological findings, *Women and Men* has not been surpassed. By starting with the biological bases of reproduction, sex determination, and sex linkage, Scheinfeld supplies the outstanding lack of Havelock Ellis' now classical works on sex. The extensive data on the comparative growth and development of pre-adolescents gathered in the past ten years has been summarized and evaluated in several chapters. The emphasis on the male as, although the stronger, yet the more delicate sex will be new to many readers, but is quite sound. Scheinfeld brings out the basic sex differences in intelligence tests, the effect of which on the measurement of the I.Q. is suppressed by the design of the tests and the selection of items. Puberty is discussed, and emphasis is placed on its average arrival two to three years earlier in girls than in boys, thus affecting social relations and marriage between different age groups, and education. "Not only is the girl less intellectually mature when important social problems confront her, but her errors, missteps, or transgressions may have far more serious consequences."

Adult sex differences are also discussed first from the biological point of view, ranging from hormones, skeleton, and fingerprints to disease resistance and susceptibility, and life expectancy. As to behavior, the emphasis falls on its conditioning because of physical differences, and the consequent progressive divergence of behavior patterns with increasing age. Sex life and homosexuality, crime and punishment for crime, dress, the division of labor, achievement and genius are successively considered from this point of view. The author regards male dominance and chivalry as having roots in pre-human behavior, and equality for women, in a literal sense, as both undesirable and impossible. The outcome of the Soviet experiment has helped to show that a double standard is inevitable, as long as only women bear children. Yet Scheinfeld is not biased. He does not regard a double standard as implying inferiority or justifying underprivilege on either side, and concludes with advice that takes cognizance of the difference between mothers and childless women in the society of today.

Every college student should be required to read this book. Every intelligent man and woman will find it instructive and thought-provoking. It should have a great and a prolonged influence.

BENTLEY GLASS

ENVIRONMENT, RACE, AND MIGRATION. *Fundamentals of Human Distribution: With Special Sections on Racial Classification; and Settlement in Canada and Australia.*

By Griffith Taylor. The University of Toronto Press, Toronto. $3.50. xv + 483 pp. 1937.

This is in reality several books in one, as is indicated by its subtitle. It is composed of much previously published material, with some additions. As Taylor states in his preface, it is in a sense a new edition of his *Environment and Race*, published in 1927.

Fully half of the book deals with the problems of racial classification. Taylor's contribution is the application of the theory of age and area to the races of mankind. He conceives of mankind evolving in central Asia, with races spreading out therefrom like ripples caused by a stone cast into a pool. The first waves are primitive, the later progressively more evolved. By pointing to the geographic position of the various races of mankind, he is then able to place them in a series from the most primitive (Negrito) successively through Negro-Melanesian, pre-Dravidian-Australoid, and Mediterranean, to Alpine-Mongoloid. This last race, he points out, is the latest development in Asia, and is therefore the highest form of man yet evolved. By extension of his reasoning, any race in a refuge area is an early and biologically primitive race. He advocates the use of geographic location as a trait in racial classification of equal value to the usual biological characters!

Taylor's discussion and mapping of the distribution of the races is always interesting and often stimulating. There is sufficient truth in the doctrine of age and area, and in the significance of the zoning of races that Taylor's work can not be summarily dismissed. Many, however, will wish that the author showed a broader understanding both of physical and cultural anthropology. Few will be willing to accept the doctrine of all evolution of man occurring in Central Asia. Few indeed will be willing to accept his ranking of races as biologically superior and inferior; least of all on the inadequate data presented. For example, according to Taylor a primary measure of racial superiority is survival, thus, the extinction of the stone age Tasmanians by the iron age Englishmen is proof of the biological superiority of the Englishmen.

The entire book, but especially those sections dealing with racial questions is pervaded with geographic-environmentalism. Huntington's theories of stimulating mid-latitude climates versus stagnating low-latitude climates are followed and elaborated. The relationship between temperature and mental and physical energy is considered proved. Huntington's map showing mortality in the United States is reproduced to help prove the effects of good and bad temperatures. However, close comparison of the mortality map with maps of such climatic factors as seasonal temperatures, rainfall, sunshine, etc., actually shows there is no correlation. Furthermore, other mortality tables give utterly different distributions.

Taylor's handling of physical data so as to achieve a fit with cultural data is well exemplified in his development of an index, the econograph, for measuring the potential occupation of regions. On page 439 he states that by trial-and-error juggling of the weighting principally of temperature and rainfall figures he achieved what was to his mind a ratio that gave a good fit with the observable population densities in fully developed regions. On page 448, the validity of this measure is assumed to be established because it fits a fully developed region. But this is shooting your decoys and proves nothing. In practice, the econograph figures give such startling results as placing Southern California and the Congo in the same class.

The book is biologically and culturally unsound. Taylor's geomorphology and climatology are good. His attempts to go from that base into biology, anthropology, linguistics, human geography, and the prediction of future populations are highly unconvincing.

GEORGE CARTER

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THE ANTHROPOLOGY OF KODIAK ISLAND.

By Aleš Hrdlička. The Wistar Institute of Anatomy and Biology, Philadelphia. $5.00. xix + 486 pp. 1944.

The late, distinguished author had undertaken a systematic anthropological survey of Alaska during ten summers between 1926 and 1938, measuring living natives and excavating skeletal remains of their predecessors. He soon had reached the conclusion that human migration from eastern Asia to the New World had been a continuous process extending over thousands of years, and had included a variety of physical types and of material cultures. These migration waves hardly penetrated the inhospitable Alaskan mainland, but followed preferably the more inviting coastal region southwards. On the latter route the large Kodiak Island with its comparatively mild climate and good food resources appeared as one of the most promising places for the anthropological explorer. When the Russians discovered the island in the middle of the eighteenth century, they found it populated by a large tribe, the Koniags, numbering about 10,000.

Hrdlička's field work, concentrated on Kodiak Island from 1931 to 1937, produced the results he had hoped for in the form of skeletal and cultural material and permitted many conclusions concerning the racial history of southwestern Alaska and of Kodiak in particular. As early as post-glacial conditions made it possible, the island became inhabited by man. First came the Pre-Koniags, early Asiatic immigrants, resembling somewhat Eskimos and more so Algonquin Indians, but culturally a group of its own. They were remarkably uniform in type and brought with them a chipped-stone culture and a high artistic ability. They fashioned ornate stone lamps and fine bone plates, they buried their dead, but they also seem to have practised cannibalism. They occupied the island for perhaps twelve to fifteen centuries during which time their culture gradually changed, though remaining distinctive. In Hrdlička's words, "They, however, rather degenerated in some ways, eventually fighting and massacring their own kind..." At a more recent epoch these ancient inhabitants disappeared, to become replaced by the Koniags, a cruder people, less artistic, but not cannibalistic. Physically the Koniags fall between the Aleuts and the southern Alaska Indians, with whom they form a single group which is derived by the author from the large Tungus stock of northeastern Asia.

The first part of the volume collects historical data concerning the people of Kodiak Island, their appearance and mode of life in the early Russian days. A short, second part describes the author's surveys of the island and the neighboring mainland. The record of these pioneering efforts will benefit future archeologists. The large, third part is devoted to Hrdlička's actual excavations on the island, discussing not only significant finds in detail, but describing also the daily occurrences during the field work, diary notes on weather, food, insect pests, and on all the many disappointments and thrills connected with exploring. The fourth and scientifically most valuable part (79 pages) records the physical anthropological data on the few living remnants of Koniags and on the rich collection of skeletal remains of these islanders and of their precursors.

The book is generously illustrated with more than two hundred photographs, of which those taken in the field are mostly amateurish and somewhat disappointing. This posthumous publication is of value not only to the author's professional colleagues, but also to that rapidly growing number of people interested in Alaska, the conditions of life to be encountered there, and the history of its early inhabitants.

Adolph H. Schultz

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The Conflict between the California Indian and White Civilization: *I. The Indian Versus the Spanish Mission. II. The Physical and Demographic Reaction of the Non-mission Indians in Colonial and Provincial California. III. The American Invasion, 1848–1870. IV. Trends in Marriage and Divorce Since 1850. Ibero-Americana: 21–24.*
By S. F. Cook. University of California Press, Berkeley and Los Angeles. $2.00; 50 cents; $1.25; 35 cents (paper). 194 pp.; 55 pp.; 115 pp.; 29 pp. 1944.

This series of essays in ecology and human biology examines the reaction of a primitive population to a new and disturbing environment, in quantitative terms. The most obvious result of the white invasion of California is the tremendous decline in the aboriginal population. In the Spanish missions, in the course of about 60 years, a reduction of 72 per cent took place. The wild tribes in contact with the Spaniards lost "only" 62 per cent. In the early American period (1848–1865) the annual rate of depletion even rose threefold, as compared to the Spanish-Mexican years. Disease accounted for 60 per cent of the losses, armed conflict for only 11.5 per cent. Dietary maladjustment is difficult to assess, and in this field the compensatory reactions of the Indians (cattle-theft, gathering of wild foods, use of white waste material) were perhaps most successful. The problems created by imposing absolutely new values in the field of labor and sex on a primitive population (including the wholesale rape of Indian women during the early American years) are duly analyzed by the author.

It is impossible to do justice in a short review to this pioneer effort, equally important for the anthropologist and the human biologist. For at least one region the great tragedy of the destruction of an aboriginal population by whites is lifted from a merely descriptive level to one of fruitful and exact scientific analysis. With great ingenuity sound quantitative material is traced and combined. The author's attempt to describe in purely biological terms processes which, at least at the present stage of our knowledge and in the author's own opinion, are not purely biological, leads sometimes to stylistic oddities which are of but minor importance.

From an editorial point of view, it is hard to understand why the first three essays have not been published as the one single volume which they actually form. Essay No. IV is an interesting short paper on the changes in Indian marital mores under the impact of white civilization.

Erwin H. Ackerknecht

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The Navaho Door. *An Introduction to Navaho Life. By Alexander H. Leighton and Dorothea C. Leighton. Harvard University Press, Cambridge.* $4.00. xviii + 149 pp.; 33 plates. 1944.

This little book is destined to give to Indian Service workers a better understanding of the mentality of the Navaho, at present the largest Indian tribe in the United States (50,000 members), and to teach better methods in bringing our type of civilization to a minority with an entirely different cultural tradition. It describes the environmental, historical, and ideological background of the Navahos. It sketches the present administrative setup. The authors outline, on the basis of their own rich personal experience, methods for getting the Navaho to accept white medical care in the hospital and out-patient work without coercion, and to use elements of his own cultural legacy. Three Navaho life histories illustrate the more general statements of the authors, and are of great documentary value.

The book, well written and splendidly illustrated, will find interest far beyond the circle of Indian Service workers. It is important to all those working on minority problems. It is most valuable reading for the professional social anthropologist. As a matter of fact, this study by two psychiatrists is one of the best anthropological publications of the last several years.

ERWIN H. ACKERKNECHT

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RACIAL PREHISTORY IN THE SOUTHWEST AND THE HAWIKUH ZUNIS. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XXIII, Number 1.*

By Carl C. Seltzer. Peabody Museum of American Archaeology and Ethnology, Cambridge. 75 cents (paper). vii + 37 pp. 1944.

An analysis of skulls of the Old Zuni Hawikuh, a sixteenth century Indian group, showed the physical type to be of a highly distinctive character. The distinctive features were small-headedness, short skull lengths, narrow skull widths (cranial index bordering on the dolichocephalic side of mesocephaly), high skull vaults, long total facial and upper facial heights, narrow facial widths.

These characters were distinctive enough to encourage the author to try to find other Southwestern groups of similar type. Comparisons were made with three Basket Maker groups: Grand Gulch, Arizona Basket Makers, and Hooton's "Basket Maker" segregates from the Pecos material. The first two groups are of considerable antiquity and represent the people who held the Southwest from at least the time of Christ and probably for a long prior period. The relationships between the groups was shown to be very close. The Grand Gulch Basket Makers and the Zuni are shown to be nearly identical in sixteen measurements and eight indices. Similarly, striking resemblances were shown for the other groups.

The comparisons were then extended, and the Zuni skull series was compared with skulls from Salt River Valley, Chaco Canyon, Petrified Forest, Chaves Pass, and Puyé. In comparing these groups, composed entirely of artificially deformed crania, with the Zunis it was necessary to omit the dimensions of the skull vault and to resort to the diameters and proportions of the facial skeleton, skull base, and expressions of general head size. The result was the demonstration that the Zuni were not a unique type, but that they represented a type widely distributed in the Puebloan Southwest. It is equally clear that this type is the ancient type in the Southwest, and has persisted with little change. Further comparisons, particularly with Hooton's work at Pecos on the eastern side of the Pueblo area, showed that the only evidence for sweeping changes in physical type came very late in the Pueblo period and was seemingly due to an influx of peoples from the Plains area to the north and east.

These findings are at complete variance with the American anthropologists' long established dogma of the occurrence of a sweeping change in physical type at the time of the cultural shift from Basket Maker to Puebloan culture. Seltzer's work is statistical, his tables are presented, and his conclusions are thus subject to immediate check. It is obvious that Seltzer is correct and, as he points out, the Southwestern anthropologists have been guilty of very loose use of such terms as long heads and round heads.

This is, then, a most valuable paper, if only because it clears out a mass of assumptions and sets us on a sounder footing. It is also of theoretical interest to all students interested in rates of change of physical type over periods of time.

GEORGE CARTER

* * *

THE INDIAN BACKGROUND OF COLONIAL YUCATAN. *Publication 548.*

By Ralph L. Roys. Carnegie Institution of Washington, Washington. $2.75 (cloth); $1.75 (paper). vii + 244 pp.; 2 maps; 6 plates. 1943.

When Francisco Hernandez de Cordoba discovered Yucatan in 1517 he found evidence of a culture definitely superior to any which the Spaniards had previously met in the new world. The purpose of Roy's excellent book is to draw a picture of what was actually still alive of Maya civilization, the highest preColumbian development we know of, at the time of Spanish conquest. The author reviews all possible aspects of the problem such as social and political organization, customs, agriculture, industries, commerce, religious and scientific lore, etc. Though many of Mr. Roy's data have been available already in the works of Gann, Means, Thompson, Tozzer, and others, his systematic survey is a most welcome contribution to Maya studies. The most original parts of the book are an analysis of the integration of the native nobility into the Spanish governmental structure, and of the Mani land treaty of 1557, the earliest authentic Maya document written in European script. Beautiful illustrations, a glossary, bibliography, and index complete the valuable publication.

ERWIN H. ACKERKNECHT

* * *

ARCHAEOLOGY OF NORTHWESTERN VENEZUELA. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XXVI, Number 1.*

By Alfred Kidder, II. Peabody Museum of American Archaeology and Ethnology, Cambridge. $3.75 (paper). viii + 178 pp.; 1 map; 18 plates. 1944.

This is a technical archeological paper. It is based on field work done by the author in northwestern Venezuela at various widely distributed sites. The principal work was done in the vicinity of Lake Valencia in the northern part of the country. Here extensive excavations were made.

In addition to excavations, the literature of the early historic contacts with the Indians is surveyed, the published work of the other workers in the field is included, and many of the collections of fellow archeologists were studied. The principal part of the publication is, however, a careful and detailed presentation and discussion of the artifacts recovered and the burial practices met with at the different sites. There are ample, excellent illustrations. No data is given on the abundant skeletal material excavated.

It is clear that Venezuelan archeology, although it presents a most attractive field for study because of its geographic location in a crossroads position, has been badly neglected. This work serves to indicate the presence of several treams of influence. The presence of Amazonian, Central American, and Middle American influences are noted. The author uses excellent judgment in refusing to push his correlations. He does outline possibilities and probabilities, and indicates what is needed in the way of future work. This publication will be basic to future archeologic work in Venezuela.

George Carter

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The People of Alor. *A Social-Psychological Study of an East Indian Island.*

By Cora Du Bois. With Analyses by Abram Kardiner and Emil Oberholzer. University of Minnesota Press, Minneapolis. $7.50. xvi + 654 pp.; 32 plates. 1944.

Alor is a small island of the Netherlands Indies about half-way between Java and New Guinea. Its people are Melanesians who have been influenced by the higher cultures and races of the Greater Sunda Islands.

The book comprises four parts. In the first part, which is short, the author and Abram Kardiner state the problems. This is followed by a description of the social structure of Alor. Part Two, entitled "Psycho-Cultural Synthesis," presents the cultural material which is organized about the life cycle of the individual. Here we follow the Alorese from birth to death and learn about their relation to the various institutions of their society at each stage.

Part Three, which makes up more than half of the volume, contains eight autobiographies collected by the author. These are important contributions to our knowledge of how primitive peoples think and feel. Each biography is followed by a psychoanalytic analysis from the pen of Abram Kardiner.

Part Four, "Descriptive Norms and Ranges," presents the results of Porteus Maze Tests, word associations, and children's drawings, and an interpretation of the Rorschach experiment by Emil Oberholzer. The book is the product of full collaboration between an anthropologist on the one hand and psychologists on the other.

The People of Alor belongs to those studies which deal with the interrelations of culture and personality. Different societies have different basic, or *modal*, personalities (the term *basic personality* was coined by Kardiner, while the term *modal personality* was coined by Du Bois). These cannot be explained by inherited racial characteristics. They are the result of common cultural pressures upon the developing individual. The central task of the author consists therefore "of tracing through with as much consistency as possible the repeated and standardized experiences, relationships, and values which occur in many contexts and to which most individuals are exposed during various stages of their development, when their resources vary."

The book is a most valuable source of ethnographic material about institutions, as the informants freely described these, whereas they were reluctant—the men less so than the women—to discuss their inner feelings and reactions. The author used the technique of the psychoanalytic interview and met her informants for one hour in the morning. Each session began with the narration of the dream of the previous night. This procedure was facilitated by the Alorese habit of remembering and discussing dreams. The informant was encouraged to talk about his childhood and describe his feelings.

The results of the various approaches to the Alorese personality—involving close collaboration between several experts and the use of scientific methods—show a fundamental agreement.

It is certain that this book will become a classic among studies of the relationship between culture and personality.

K. J. Pelzer

◆

The Peoples of French Indochina. *Smithsonian Institution War Background Studies Number Nineteen.*

By Olov R. T. Janse. Smithsonian Institution, Washington. 25 cents (paper). iv + 28 pp. 1944.

Recent events have brought French Indochina into the limelight, so that this well illustrated booklet in the series of War Background Studies published by the Smithsonian Institution proves extremely timely.

French Indochina comprises four protectorates—Tonkin, Annam, Laos, and Cambodia; one colony, Cochin-China; and the leased territory of Kwangchowan on the Luichow Peninsula of the Kwangtung Province. After a brief resumé on topography, climate, hygiene, natural resources, transportation, harbors, and history, the author deals with the various racial groups of Indochina. Since time immemorial Further India has been a crossroads of peoples and cultures. The peoples of Indochina may be divided into two main groups: 1) the peoples of the plains and the Mekong valley, and 2) the peoples of the mountains. Numerically the most important people are the Annamites, who are culturally and physically closely related to the Chinese; they number about 17,000,000 souls or nearly three-fourths of the total population. They live in the plains of Tonkin, Annam, and Cochin-China. Next in importance, both politically and culturally, are the Cambodians, who number about 3,000,000. Their home is the lower Mekong Valley, especially that part included in Cambodia. They are believed to be the descendants of the Khmers, the builders of the famous monuments of Angkor. The Cambodians at one time controlled a much larger territory, but their neighbors, the Thai and Annamites, forced them to give up some of the richest sections of their kingdom.

Scattered among Cambodians and Annamites live the remnants of the once mighty Cham (some 100,000 souls), the past rulers over large parts of Annam and Cochin-China. Other important peoples of the plains are the Laotians, the Chinese—most of whom are immigrants or descendants of recent immigrants—the Malays, and Indians.

The two-and-a-half million mountain people comprise a whole series of tribes that can be divided into two groups, a northern and a southern group The northern group is formed by tribes who immigrated in historic times from southwestern China, while the southern group comprises the real aborigines of Indochina, the Indonesians—also referred to as proto-Malays or Moï. While the plains people are permanent-field cultivators who grow lowland rice especially, the majority of the mountain folk are shifting cultivators who plant chiefly upland rice, corn, sweet potatoes, and beans in a forest clearing, or *ray*.

Since the publication of this study, France has announced that after the present war French Indochina will become the first dominion in the French Commonwealth of Nations. Will France be able to carry out its promise of "no racial, religious or national discrimination" in the face of a very aggressive Annamite majority which considers itself far superior to all other indigenous racial groups?

K. J. Pelzer

Early Man and Pleistocene Stratigraphy in Southern and Eastern Asia. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XIX, Number 3.*

By Hallam L. Movius, Jr. Peabody Museum of American Archaeology and Ethnology, Cambridge. $3.75 (paper). ix + 125 pp.; 1 map; 1 table; 18 plates. 1944.

This is a synthesis of the recent work in the paleolithic archeology of southeast Asia. It is of great value in that it brings together a mass of scattered papers and presents the results in an orderly and digested form. The grasp of the material is greatly aided by large figures that show the correlation of geology, climate, fauna, and archeology.

The discussion is regional. Northwest India, Upper Burma, Northern China, and Java are considered in turn, their probable correlations are discussed, and then the general problem is summed up. For each area the geologic happenings of the Pleistocene are discussed, and the paleolithic implements are placed within this framework. It is the author's contention that one can not order cultures primarily by their artifacts, since these are essentially social phenomena. One must depend on such natural science aids as geology, climatology, glaciology, and paleontology. By using these aids, Movius makes a generally convincing effort to show the relations between the various cultures of the areas discussed.

From this work one gets a view of the differences in the culture developments of southern and eastern Asia as opposed to the developments of Europe and Africa. Asia is characterized by a chopping-tool complex quite different from the European. It is pointed out that this is correlated with different types of men, the Sinanthropus-Pithecanthropus men as opposed to the European paleolithic men.

The divisions of the Pleistocene used are: lower Pleistocene, first glacial and interglacial; middle Pleistocene, second glacial and second interglacial; upper Pleistocene, third glacial, third interglacial, and fourth glacial. This seems an unusual division, for it shortens the lower Pleistocene and lengthens the upper. If one follows the theory recently elaborated by Simpson of the origin and divisions of the glacial period, it is much more reasonable to place the first two glacials in the lower Pleistocene, the second interglacial then becomes the middle Pleistocene, and the last two glacials make up the upper Pleistocene. Movius' evidence makes it very clear that the second interglacial is of great length in Southeast Asia. His temperature and pluvial data also fit the Simpson theory. Although this is largely a matter of terminology, it also affects somewhat the relative antiquity of the cultures involved.

George Carter

BIOMETRY

Vital Statistics of the United States 1942. *Part II. Natality and Mortality Data for the United States Tabulated by Place of Residence.*

Prepared under the supervision of Halbert L. Dunn. U. S. Department of Commerce, Bureau of the Census; United States Government Printing Office, Washington. $2.00. iii + 533 pp. 1944.

In 1937 the Vital Statistics Division undertook the difficult but important step of tabulating the birth certificates by residence of the mother and the death certificates by residence of decedent. These tabulations did not replace those hitherto made on a place-of-occurrence basis, but rather supplemented them. The annual statistics have, since that date, been published in two volumes, Part I being on a place-of-occurrence classification and Part II on place-of-residence. The present volume is Part II for 1942.

The value of this new series on a residence basis is very considerable. The development of strong urban hospital centers and the general lack of hospital facilities in rural areas have been important factors in drawing people to the cities for medical care. When the births actually occurring in the cities are divided by the urban population, as was done prior to 1937, a birth rate is obtained that exaggerates the rate of reproduction in the area. There is, of course, a corresponding deficiency in the rural rate when computed on this basis. For many, although not all, purposes rates on a residence basis are a more satisfactory index of the vital facts for a population than those on occurrence. For certain studies, such as use of hospital facilities, the differences between the occurrence and residence figures are of importance.

Some indication of the amount of re-allocation is given by the following figures: Of approximately 1,400-000 deaths in 1942, about 250,000 or 18 per cent occurred in a place other than the usual residence, and of the 2,800,000 births, more than 700,000 or 26 per cent occurred away from the usual place of residence of the mother. Of the births to rural residents, 30 per cent occurred in urban areas, making the births occurring in urban areas 22 per cent higher than those to residents alone. There is a large variation between states as to the importance of residence allocation; in some cases, the difference between occurrence and residence figures is much larger than those quoted for the country as a whole, while in others the difference is trivial.

The vital statistics are presented in thirty-one basic tables, in which live births, stillbirths, total deaths, and infant deaths are subclassified in considerable detail on geographical and biological axes. These cannot be enumerated completely here, but their scope may be indicated by a partial list of classifications for live births. These include sex of child; age, race and nativity of mother; order of birth, month of birth, cases of plural birth with number born alive and stillborn; state of residence by urban and rural areas, and attendance at birth. Many of these items are cross-tabulated. Almost equally extensive tabulations are given for the deaths.

Students of the dynamics of population will be gratified that the war has not necessitated the breaking of this excellent series of annual publications.

MARGARET MERRELL

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

ARCTIC MANUAL.

By Vilhjalmur Stefansson. The Macmillan Company, New York. $3.00 xvi + 556 pp. 1944.

Prepared for the Army Air Corps by the great Arctic explorer, Vilhjalmur Stefansson, and his staff, no one will question the authoritative character of this book. When it is added that it surveys all aspects of life in the North and that it is readable and well organized, no higher praise is needed. Its one notable omission is illustration. Except for the thirteen plates of photographs showing how to build a snowhouse and to make a snow camp, the book is without pictures. Yet something had to be sacrificed to provide so full a manual of information at so reasonable a cost.

The chapters deal with the region's historical background; physical geography; climate and weather; natural light; animal life; vegetation; shelter, heat, and artificial light; food and drink; clothing and personal equipment; health, accident, and disease; travel; transportation; hunting and fishing; and mechanized transport. Biologists will be specially interested in the notes on wild and domestic animals, fishes, and insect pests and parasites. Stefansson's observations include many that are new and valuable. The discussion of vegetation is less extensive but also illuminating. The chapter on climate and weather is of ecological significance; that on health, accident, and disease has information on diet, exercise, first aid, diseases, and monoxide poisoning.

The extraordinary interest of this book is apparent at almost any page to which one may open. Whether it is a brief discourse on eating fat, the importance of keeping clean shaven, colds, or the selection of dogs, the remarks are pungent and clear as Arctic air, flavored with good humor and keen understanding.

BENTLEY GLASS

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THOMAS JEFFERSON AND THE SCIENTIFIC TRENDS OF HIS TIME. *Chronica Botanica, Volume 8, Number 3. By Charles A. Browne. The Chronica Botanica Co., Waltham; G. E. Stechert and Company, New York.* $1.25 (paper). 361–424 pp. 1944.

It is the introduction of Browne's little monograph, rather than the bulk of his study, which corresponds exactly to the title of his booklet. In the introduction Jefferson is shown as one of the numerous statesmen-scientists of his time. The utilitarian and conservative character of Jefferson's scientific orientation are emphasized. Then Jefferson's *Notes on the State of Virginia* are analyzed for their scientific content and merits. Jefferson's role as promoter of science while President of the United States is recorded. Special attention is given to Jefferson's achievements as a scientific agriculturist. The study ends with a description of Jefferson's work in furthering scientific education. Nothing essentially new is added to the extensive literature on Jefferson, the scientist; but the excellent standards of scholarship displayed, the adequate presentation of a fascinating subject matter, the easy accessibility of material, otherwise rather hidden or widely dispersed, will undoubtedly make many friends for this little book.

Erwin H. Ackerknecht

A Survey of General and Applied Rheology.

By G. W. Scott Blair. Pitman Publishing Corporation, New York. $4.00. xvi + 196 pp. 1944.

Rheology is defined by the author as the study of the "flow and deformation of matter," or more narrowly, of the "stress-strain-time relations" in materials with "behaviour intermediate between those of solids and liquids." To biologists interested in the physical characteristics of protoplasm or protoplasmic products, this introduction to the science should be highly valuable.

The volume opens with a historical introduction, of general interest. Biologists, in particular, will find instructive the discussions of irreversible breakdown, structural viscosity, thixotropy, false body and related and converse phenomena; of mesomorphic states, tactoids, and coacervates. Aerodynamics, the rheological properties of polymers, and other topics discussed adequately elsewhere are not included. In part II, first, rheological interpretations are examined from the points of view of theory and practice; and second, considerable space is devoted to the place of "psychophysics" in rheology. Without question, subjective judgments based on differences in perception must play a significant role in this science. Scott Blair's experimental approach to the study of these is most interesting. In another chapter, the author undertakes to apply Gestalt psychology to rheology, reaching the conclusion that qualities such as "tackiness" have the nature of a Gestalt, and, in general, that each unit is to be appreciated in its spatial and temporal context.

This book could be critically appraised only by a team comprising at least a physicist, a biophysicist, and a psychologist. It is, however, apparent that it will be interesting to many biologists. The integration of special sciences undertaken by the author should prove most stimulating.

Bentley Glass

Meet the Electron.

By David Grimes. Pitman Publishing Company, New York and Chicago. $2.00. vii + 120 pp. 1944.

For laymen, the author has surveyed the science of electronics in simple language and with graphic illustrations. This is just the book for a high school student or college freshman who is becoming interested in electronics, or for anyone with little or no acquaintance with physics who desires an introduction to a field of rapidly enlarging utility. It will not be of much value to biologists.

Photomicrography in Theory and Practice.

By Charles Patten Shillaber. John Wiley and Sons, Inc., New York; Chapman and Hall, Ltd., London. $10.00. viii + 773 pp. 1944.

The art of photomicrography involves three important steps, namely, correct manipulation of the microscope, a thorough understanding of lighting techniques, and the mounting and handling of specimens on the microscope stage. As the author points out, in most cases failure to produce good negatives is the result of poorly aligned equipment. One of the aims therefore of the present volume is to instruct the reader in the proper and precise alignment of all optical parts. Since this necessitates a thorough knowledge of the construction and function of the various elements of the optical system, the greater portion of the book is concerned with this important topic. Throughout the text there has been no separation of photomicrography and microscopy, since the same fundamental knowledge applies equally to both. In photomicrography, the sensitive film replaces the eye.

Space has been wisely given to a discussion of mounting media, stains, reagents, and solvents, and their purpose and application in photomicrography. "The photomicrographer should have a general bird's-eye view of the possibilities of all mounting methods as applied to various branches of medicine, minerology, metallography, and other scientific studies, to the end that he will be able to adopt or adapt, wholly, in part, or in combination, the various techniques of staining, etching, chemical reaction or crystallization for his own purpose."

The final chapter is devoted to an analysis of practical photomicrographical problems. A wide variety of specimens and the techniques involved in their handling is very well illustrated. It is here that the majority of the 140 photomicrographic illustrations appear. Several of them show the results of specimens under varying techniques, lighting arrangements, lens systems, etc. For convenience this chapter has been divided into eight parts depending upon the type of specimen and the microscopic technique involved, e.g., specimens photographed at magnifications of 50 diameters or less; histological specimens; metallographic and petrographic specimens; etc.

While the author is to be highly commended for his unusually clear treatment of a very technical and difficult subject, it is regrettable that he purposely chose to omit any mention of branches of photomicrography such as work with polarized light, color photography, ultraviolet and infra-red radiation, and stereoscopic pictures. However, in spite of this omission the volume is a most welcome contribution to microscopy and photomicrography. The wide variety of useful information together with an abundance of well chosen illustrative material in the form of photographs of apparatus, diagrams, tables, etc., all go to make this book especially desirable for beginners, teachers, and the more professional microscopist and photomicrographer.

John Spurbeck

◆

Nature and Camera. *Summing Up Fifty Years' Experience of Photographing Flora and Fauna.*
By Oliver G. Pike. The Focal Press, London and New York. 13s 6d. 262 pp. 1943.

One hundred and fifty-seven photographs, numerous pictorial diagrams and, most important of all, fifty years of experience in nature photography are condensed into this relatively small volume, providing much useful information for those interested in taking pictures out of doors.

The well-chosen photographs by the author and other prominent nature photographers illustrate the great variety and wide range of pictorial expression in this field. The author points out that the development of modern miniature cameras, roll film, exposure meters, and range finders is of great advantage in that it enables the photographer to devote more freedom and attention to the subject itself, whether bird, flower, or beast.

After a brief discussion of the equipment necessary in nature photography, the author gives concrete suggestions on the actual methods of procedure with various natural subjects such as flowers, birds, bird nests, mammals, fish, reptiles, insects, etc. From all of this we are led to see that nature photography is more a blend of the right approach and a few simple "tricks" than an elaborate specialized technique. Given the time and patience and the desire to study habitats of natural subjects, almost anyone who knows how to use a camera at all can develop an interesting hobby and obtain unusual and original photographs.

◆

Hackh's Chemical Dictionary *(American and British Usage) Containing the Words Generally Used in Chemistry, and Many of the Terms Used in the Related Sciences of Physics, Astrophysics, Mineralogy, Pharmacy, Agriculture, Biology, Medicine, Engineering, etc. Third Edition.*
Edited by Julius Grant. The Blakiston Company, Philadelphia. $12.00. xii + 925 pp. 1944.

This complete revision of an indispensable standard work has been carried out, following the death of Ingo Hackh, by his British collaborator in the earlier editions. By omitting pronunciations, as to which every scientist is a law unto himself anyway, space has been saved for many additions without increasing the bulk of the volume. It now includes over 57,000 definitions. Special effort has been made to balance British and American points of view. Probably no reference book will be more generally useful to the biologist than this. It contains not only definitions of chemical and physical terms, with numerous tables, illustrations, and diagrams, but also much biographical and biological material. Its standard of accuracy is high. Its type is well chosen for legibility.

◆

Pacific Ocean Handbook. *Second Edition.*
By Eliot G. Mears. James Ladd Delkin, Stanford University. $2.00 (cloth); $1.00 (paper). x + 198 pp.; 1 map. 1944.

This little handbook presents a wealth of facts pertaining to the Pacific area. It is profusely illustrated with maps, charts, diagrams, and a large insert containing global views of the Pacific from the west, east, and center. There are sixteen chapters describing various oceanographic, climatic, and geographic features of the Ocean and its coastlines. Such topics as volcanoes, earthquakes, tides, currents, winds, storms, temperature, precipitation, fog, and geomagnetism are briefly discussed. In addition, there are short references to the major ports on both sides, some pointers on navigation, and on the characteristics of sea water. Twelve appendices give further factual data on areas and population, airline distances, food plants and animals, hints for the shipwrecked, etc. It is obvious that to cover so much material intensive condensation was required, and in some sections the presentation suffers accordingly. However, it should provide helpful information to those now active in the Pacific area. "The second edition has been enlarged to include additional information, appendices on coral islands and on monsoons, as well as a more complete index. The majority of maps have been redrawn to make them clearer . . . " The author will welcome information based on first-hand observations and experiences within the Pacific area.

◆

Annual Report of the Board of Regents of the Smithsonian Institution *Showing the Operations, Expenditures, and Condition of the Institution for the Year Ended June 30, 1943. Publication 3741.*
United States Government Printing Office, Washington. $2.00. xi + 609 pp. 1944.

In addition to the annual report, this volume contains an appendix of twenty-three papers of considerable general interest. Three of these, "The Natural History Background of Camouflage" by Herbert Friedmann, "Dangerous Reptiles" by Doris M. Cochran, and "Origin of the Far Eastern Civilizations" by C. W. Bishop are reprinted from the excellent series of Smithsonian War Background Studies. Other papers of biological interest deal with the biological effects of solar radiation, plants of China and their usefulness, natural rubber, lessons from Old World land use, areal and temporal aspects of South American culture, culture contours in Indonesia, the Arab village community of the Near East, chemotherapeutic agents from microbes, sulfonamides in the treatment of war wounds and burns, the yellow fever situation in the Americas, and food problems of wartime. Other articles deal with solar radiation for power, oceanography, petroleum geology, maps, synthetic textile fibers, new metals, and the sea as a storehouse of materials.

The style of the papers is in general non-technical, resembling that of articles in the *Scientific Monthly.* Numerous plates and maps help to make the discussions informative. Altogether, it is a volume that will be stimulating and useful to the biologist.

MAUD DE WITT PEARL

MAY 3, 1879—AUGUST 10, 1945
ASSISTANT EDITOR OF THE
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THE QUARTERLY REVIEW of BIOLOGY

MIMETIC POLYMORPHISM, A CONTROVERSIAL CHAPTER OF DARWINISM (*Concluded*)

By RICHARD B. GOLDSCHMIDT

University of California

C. *The model of other modifiers*

FISHER further considered, as a good model of what happened in the evolution of mimicry, the famous case of the inheritance of the hooded pattern of rats, as studied by Castle. A single Mendelian difference decides between hooded or not hooded, but modifiers can be selected in both directions which shift the pattern towards almost complete pigmentation or depigmentation. At one point of the discussion Fisher uses the words: "Unless the above analogies (sex and hooded rats) are wholly misleading . . ." (1927, p. 275), which might mean or not that he did not feel completely satisfied with his examples. I think that the present example is just as misleading as the former one. Nobody denies the possibility of a change of pattern by selection of modifiers. But in this case, as in so many others, the modification is of a simple linear order. The pattern determined by the allele in question varies quantitatively under the influence of modifiers (also environment in many cases) by producing more or less pigment, which spreads or retracts according to the inherited pattern. But this is not the way the pattern does change in mimicry, where completely new pattern elements, and also shapes of scales and different pigments combine to produce the new pattern. (Only certain small variations, such as those described by Ford for *P. dardanus poultoni*—see above—can be compared with the rat case; these produce small plus or minus changes of spot within the mimetic pattern.)

Ford (1940a, p. 236) used a different model, actually taken from Lepidoptera, as mentioned above. Besides his own work on *Abraxas*, dealing only with intensity of color, he cites especially the work of Federley (1920) on *Spilosoma lubricipeda* L., an arctiid moth, which has yellowish wings with small black spots. A melanic variety, called *zatima*, has practically black wings. The F_1 hybrid between both is intermediate (Ford calls it incomplete dominance of black) and F_2 segregates 1:2:1 showing a simple Mendelian factor difference, as Standfuss (1896) already knew (see Figs. 3a, 3b, 4). Later authors found modifiers for this pattern. Thus Federley found multiple modifiers as a chance find in the single pair from which all his material was derived. Goldschmidt (1924) working with material of different origin found a different genetic situation (see below). The modifiers in Federley's material shift the degree of darkness upon the wings in both directions (see Figs. 3a, 3b, 4). Heterozygotes *Zz* can show a considerable variation, according to the presence and segregation of these modifiers. By selection of the darker and lighter phenotypes, the homozygotes *ZZ* and *zz*, *zatima* and *lubricipeda*, could also be obtained in combination with plus or minus modifiers and by continued minus selection in *ZZ* almost light individuals could be obtained, while in *zz*, *lubricipeda*, the dark spots can be made to disappear almost completely. These selected types transmit their characteristics to the offspring. This case is then clearly a parallel to Castle's rats, and the same objections against a comparison with the mimetic pattern must be raised.

But Ford thinks that this example has a still greater importance for the neo-Darwinian theory of mimicry. He emphasizes that the multiple modifiers of Federley affect the heterozygote *Zz* more than the homozygous *zatima ZZ* and least the homozygous *lubricipeda zz.* "There is a suggestion therefore that the wild type form is less susceptible to the effect of genetic variability than are the heterozygous and homozygous varieties. This might be anticipated on theoretical grounds. Any successful species should be so adjusted that its usual environment represents a near approach to its optimum. That is to say, the genes ordinarily present should be selected in such a way as to produce their most favorable effects in the conditions to which a species is normally exposed. Genetic variations in the effect of wild type allelomorphs are therefore especially liable to be disadvantageous. Accordingly, we may anticipate that the reactions to which such genes give rise will have been so 'buffered' by selection that segregation within the gene-complex will produce a minimum amount of variation in the characters which they control. No such adjustment will have taken place in respect to rare varieties subject to elimination. We may therefore expect to find the latter less stabilized in respect of genetic variability than their normal allelomorphs, a condition which appears to be fulfilled" (Ford, 1940a, p. 236).

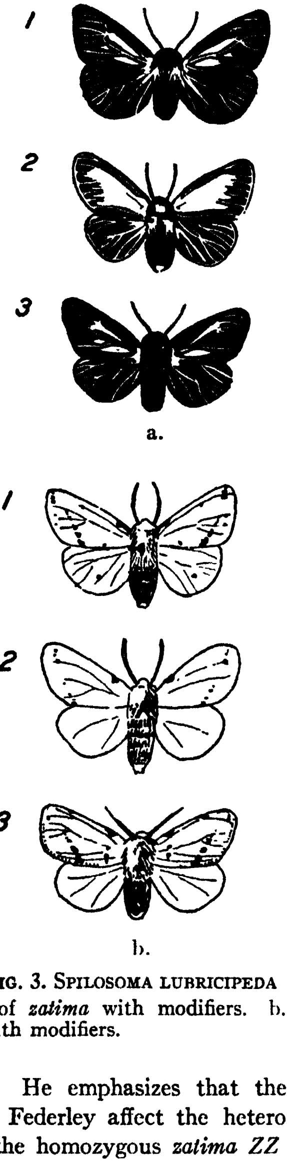

FIG. 3. SPILOSOMA LUBRICIPEDA
a. Types of *zatima* with modifiers. b. Types of *lubricipeda* with modifiers.

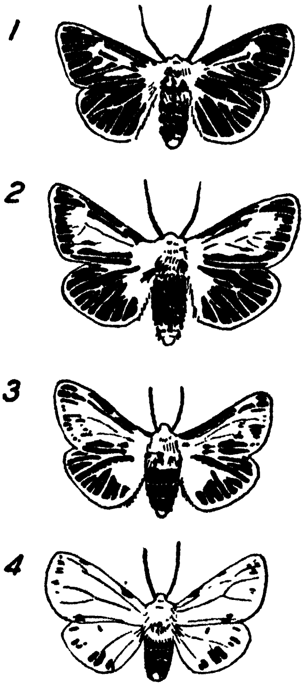

FIG. 4. DTO. F_1 TYPES WITH VARIATION BY MODIFIERS
Redrawn from photos by Federley, 1920

We have quoted Ford's argument in spite of the fact just stressed that the *Spilosoma* case has no bearing upon mimetic resemblance, because here Fisher's ideas are applied to a specific, rather well-known case, ideas which *mutatis mutandis* are the same as applied to mimicry. I believe that I can show that the neo-Darwinian explanation, just presented, is, indeed, very far-fetched and unnecessary. (1) Federley secured his modifiers only by selection from the heterozygote *Zz*, where alone he could originally discover their action. Thus we do not know whether they were introduced from *ZZ* to *zz*. All his material is descended from one pair. (2) The segregation from selected F_1 individuals showed a shift of the amount of dark pigment both in *ZZ* and *zz*. (3) Ford is much impressed by the fact that the *lubricipeda* type (*zz*) is less affected by the modifiers than the *zatima* type *ZZ*. If we look at the actual specimens we can easily see why, without appealing to theories of selection (see Figs. 3a, 3b, 4). *Lubricipeda* is characterized by a group of black spots upon a yellowish background, which form a group of rudimentary broken bands characteristic of the basic pattern of the group. The *zatima* factor produces an excess of pigment deposited almost in all cells of the wing (and also in body hair), thus covering completely the *lubricipeda* pattern. In *Zz*, this extra pigment encroaches more or less upon the light background, starting from the posterior edge of the wing. The modifiers which Federley discovered in the heterozygote (they were found only in a smaller degree in Standfuss' and my own crosses) increase or decrease the amount of pigment "flowing" over the wing. In the intermediate F_1 there is much room on the wing both for encroachment of black upon white (yellowish) and for restriction of black in favor of white. In the homozygote *ZZ* much restriction from the almost black wing is possible, but very little room is left for extension. In the wild type homozygote there is no pigment between the veins to be modified in the absence of *Z*. The modifiers therefore are either left in a void, or might act upon the small black spots of the rudimentary bands. Actually Federley found the latter. Now assume that the modifiers of a definite combination restrict the *ZZ* action by one-half. A half black wing is indeed very different from an all black one. But if the same modifiers restrict a tiny spot in *zz* by one-half, the visible change in the spot amounts to a very slight change of the total wing. The observed facts thus are simple spatial consequences of the pattern involved. If we do not look at the facts with the intention of proving a neo-Darwinian mechanism of evolution, they are simple enough and do not require any explanation of the complicated type just presented. This critique again may serve as a model for the mimicry cases. (4) There is no reason to assume that the pattern of the rarer variety is less stabilized than that of the original species. *Zatima* is actually the preponderant form in certain regions (e.g., the Friesian islands). Here the pattern is found as described (*zatima*), but also completely dark forms, called *deschangei*, occur. I was able to show that this type is based upon a multiple allele of *Z* (Goldschmidt 1924). In my material a single modifier could be seen at work, which acted, on a lower level, like those of Federley. The genetic results indicated that the modifier was present also in the wild form, but as it acted only so little upon the all dark wing it could hardly be expected that its action upon small dots would be distinguishable. Thus, all in all, I believe that the elaborate theory of selection presented by Ford for this case is completely unnecessary. Actually, wherever characters are studied which may vary in a plus or minus direction, modifiers are found which influence the phenotype. When we analyze such cases from the standpoint of developmental dynamics, we rarely find difficulties in principle for an interpretation of the resulting phenotype. There is no doubt that, under definite circumstances, such modifiers may be selected for one or the other end of the possible series of phenotypes. But this does not prove that a mutant phenotype which is adapted to certain conditions of habitat must have evolved by selection of such modifiers, if actually the mutant itself was sufficiently good as an adaptation. Such frequent types of variation found in nature as melanism, leucism, xanthism, rutilism are known to have occurred under laboratory conditions as ordinary mutants, with the maximum effect accomplished in one step. Therefore nothing else is required in nature either.

D. *Non-mimetic polymorphism*

The last sentences lead us to the general problem of polymorphism, which has been frequently discussed together with mimetic polymorphism e.g., by Ford (1940b), Goldschmidt (1940) and Huxley (1943). We point to these books for the detailed material and mention only such facts as are relevant for our present discussion. Ford (1940b) has subdivided polymorphism into four groups: (1) disadvantageous varieties eliminated by selection and maintained at a low level by recurrent mutation of the genes controlling them; (2) variations due to the effects of genes approximately neutral as regards survival value; (3) those dependent upon genes maintained by a balance of selective agencies; (4) advantageous varieties controlled by genes spreading through the population and displacing their alleles. Only the third and fourth groups are regarded as polymorphism proper; here two or more well-marked forms, capable of appearing among the offspring of a single female, occur with frequencies high enough to exclude the maintenance of the rarest of them by recurrent mutation. It is clearly Ford's third group to which the material under discussion belongs, Ford calls it *balanced polymorphism.*

But the fourth group mentioned by Ford (termed by him *transient polymorphism*) is actually the one which is most suitable to shed light also upon the third one, because here cases have been studied in which both contributing agencies, the genetical basis and the action of selection, are known. These are cases of melanism (including nigrism) in Lepidoptera. Ford (1937, p. 478) has assembled the literature on the subject of melanism —including those cases to be discussed here as well as others—and we point to his review for the details and literature. (Another discussion is found in Goldschmidt, 1940). In a general way we might say that melanic varieties falling under the above group 1 are frequent. In individual cases they may be based upon simple recessive, dominant, or multiple allelic mutants, or also upon a few collaborating or additive multiple factors. But the really interesting cases are those of so-called industrial melanism, which means the observed spread of melanic varieties in industrial districts of England and Central Europe within the last sixty years. These are the cases which comprise what Ford calls transient polymorphism. In Ford's just mentioned review all cases are assembled, and we might say, generally, that the majority of those studied genetically show that melanism is based upon dominant mutation, sometimes with multiple alleles or with additional multifactorial modifiers. I think that the best observed case, as far as the spreading of the mutant is concerned (because of its very recent first appearance at a time when attention already had been drawn to the phenomenon), is that of *Cymatophora or* (in the region of Hamburg as studied by Hasebroek). Here a simple Mendelian difference is present (as I was able to confirm in a few breeding experiments). But this form does not occur in great numbers and, therefore, cannot be observed in massed populations. Such a study is possible in the nun-moth *Lymantria monacha* L., a dangerous forest pest, appearing suddenly by millions of individuals and therefore closely watched by foresters and entomologists. Therefore much information is available upon the population side of the problem, appearance, disappearance, spreading, etc. Likewise, the genetics is well known. Melanism is mainly based here upon a sex-linked dominant (Goldschmidt, 1921). But there are also less dark types, produced by two pairs of autosomal alleles, and the maximum effect is produced in combinations of all three. It is known that the different dusky and dark forms were rare collector's specimens about a hundred years ago, which means that the three mutants (all three?) appeared from time to time but could not establish themselves. During the industrial era, and within industrial regions, this condition was completely reversed, so that now the populations contain a majority of dark forms. My own laboratory work began with thousands of pupae collected in one infested area in an industrial region. This population contained an overwhelming majority of the melanistic recombinations (grey to black) of the three alleles, while the original, recessive, white form was rather rare. But obviously it still segregated in the population. It is generally agreed that here selection was at work, and a suggestion, made both by Harrison and myself, is that the melanic mutant conferred, as a physiological by-effect, upon the caterpillars a resistance to ill-effects of feeding upon leaves incrusted with metal salts. But this case shows also how careful we must be in handling questions of selection. In the huge populations of the nun-moth found at the peak of an outbreak the selective or non-selective destruction brought about by the main known agencies does not affect the imago. More than 90 per cent of the caterpillars succumb to virus or bacterial diseases (polyhedra and flacherie). The next powerful selective factor is afforded by the larvae of beetles feeding on the egg clusters. Next come predatory beetles (like *Calosoma*), and next some birds that feed on hairy caterpillars. This shows that whatever selective advantage the melanistic mutant confers upon the imago does not work at all in the huge populations at the summit of an outbreak. But usually such pests subside after a few years, and in the interval between two outbreaks the animal becomes utterly rare, so that special attention by foresters is required to find out where it survives at all. It is in this stage of very small and restricted populations, in which disease, etc., have not much chance to be selective agencies, that the eventual small advantage conferred by the physiological adjunct of melanism, whatever it is, will work towards supplanting the original form by the melanic one. I think that this group of facts, a group in which more detailed knowledge of genetics, ecology, and working of selection is available than anywhere else, demonstrates that selection can work very fast if new situations appear and that no slow accumulation of modifiers is needed to produce the result which is reached by single mutational steps either completely or almost completely. There is no reason for supposing that cases of mimicry in which only the mimetic type exists, i.e., without polymorphism, must have originated differently.

But let us now return to Ford's group of balanced polymorphism, which comprises also the mimetic polymorphism. This type of variation is very frequent, as the examples compiled in recent books (e.g., Goldschmidt, 1940; Huxley, 1943) show. Differences in detail are found between the cases, but as to general principles the facts are comparable. We are not concerned here with the selectionist side of the problem, viz., which conditions have to be fulfilled in order to keep a polymorphic form in rather stable equilibrium. Fisher (l.c.) has worked out the statistical and ecological requirements, and those later authors who discussed this subject have accepted his analysis. The details do not concern us here, because they apply generally to balanced polymorphism whatever its genetic basis. But the genetic side is important, as it might throw light, by analogy, upon the cases of mimicry. In a general way we might say that such examples of polymorphism as have been studied genetically show that the differences between the different forms are based either upon single Mendelian differences—e.g., *Colias* (Gerould, 1921), *Argynnis* (Goldschmidt and Fischer, 1922)—or upon multiple alleles—e.g., lady beetles (Lus, 1926)—or upon ordinary Mendelian recombinations—e.g., *Callimorpha dominula* (Goldschmidt, 1924), *Helix* (Coutagne, 1895/96; Lang, 1904 ff). Using one of these examples we can devise a good analogy to mimetic polymorphism.

Already in pre-Mendelian days Coutagne (1895) found that different colonies of the garden snail *Cepaea nemoralis* contained an assembly of types, typical for each colony, but different between them. These types are based mainly upon the ground-color of the shell, the number and thickness of the bands, the interruption or confluence of bands, etc. Coutagne realized that these could be understood as permutations of a number of basic variants and actually described them in terms reminiscent of Mendelian symbols. In addition, he realized (p. 402) that different colonies had different features in other quantitative characters which are difficult of appraisal. We should call these differences today (micro-) geographical races, though an additional purely environmental effect cannot be excluded. Furthermore, Coutagne emphasized that these local characters—aside from polymorphism—were found in strikingly parallel expression in other species of snails living in the same locality. Here, then, we have a perfect analogy to the *Papilio* cases: local polymorphism, with different relative numbers of the types from locality to locality, including also localities without polymorphism; further geographic variation from place to place; and also parallelism of geographic variation with that of different species. (Recent work with similar material is reviewed by Diver in Huxley, 1940.) Later, Lang (1904 ff.) showed that a number of the individual variants were based upon simple Mendelian differences, e.g., complete bands, interrupted bands, number of bands, and union of bands, and that recombinations of these characters could be bred.

One of these recombinations permits us to invent what we consider to be a beautiful analogy to mimicry. Shells of snails may also exhibit mimicry in certain cases. Probably the most beautiful case of mimicry I have ever seen (and I have had the good fortune to see many in different climes), I found by chance when, as a young student, I was working at a Mediterranean marine laboratory. I was drawing an alcyonarian colony of special beauty, having a carmine red flesh with yellow polyps that, when retracted, appeared like yellow stars on the carmine background. Suddenly I noticed that one or two of the polyps seemed to change place, and observing more closely, I found a small snail (genus *Ovata*?) crawling slowly over the colony. Its shell had exactly the carmine color of the alcyonarian, and yellow star-like spots imitated perfectly the retracted polyps. Now to our invented analogy. Lang combined the Mendelian alleles for complete black color by fusion of the five bands with the factor for interruption of bands (dotted bands) and thus obtained cross-striated shells (Fig. 5).

It is well-known that such zebra-stripes form a powerful concealing coloration, or, in other cases, a frightening pattern (see Cott, 1940). Let us now suppose that such a shell were found in nature and in a habitat in which the zebra-pattern was actually a concealing pattern, or in association with unpalatable forms with a warning pattern of stripes; we could certainly point to a beautiful case of mimicry. Now the colony in question would segregate, if heterozygous, at least two types of non-mimetic snails besides the mimetic zebra-striped one, and a genetic analysis would discover only simple Mendelian relations. The neo-Darwinian, assuming that Lang's work did not exist, would tell us that such a huge departure from the typical longitudinal stripes of the nearest relatives of our snail as a zebra pattern, and this in imitation of a different unpalatable family, could only have been produced by a slow selection of modifiers for a zebra pattern—in spite of the simple Mendelian behavior of the patterns.

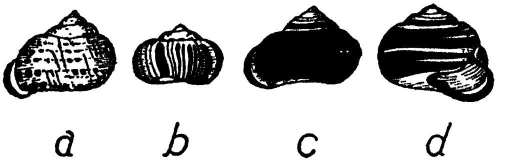

FIG. 5. CEPAEA NEMORALIS, MUTANTS FOR DOTTED (a) AND CONFLUENT (c, d) BANDS MAY COMBINE INTO CROSS STRIATION (b)
After Lang, from Goldschmidt

I do not mean to imply that the analogy could be carried on indefinitely to perfection. It is only an analogy. But it shows, I think, that a knowledge of standard cases of polymorphism makes us expect that mimetic polymorphism also originated by simple mutation or mutations of the type which Fisher calls saltation.

Thus far, we have not taken into account the fact that mimetic polymorphism occurs, in the majority of cases and in different genera and families, combined with the sex-controlled type of inheritance. This might be nothing but a matter of chance. In non-mimetic Lepidoptera, the polymorphism does affect both sexes or is sex-controlled, affecting only females. In the latter cases the deviation of the second type from the male type is not larger than that which we usually associate with a Mendelian mutation (e.g., in *Colias, Argynnis*). As some of the mimics are near relatives of these forms in which ordinary sex-controlled dimorphism exists, we might assume that a genetic constitution is present in these groups which makes mutants liable to be sex-controlled. Thus the sex-control is independent of the origin of mimetic resemblance. But we cannot help being surprised that in these cases male sex-controlled mutants or such as would affect both sexes equally or would suppress the sex control did not appear and be selected, thus providing protection also for the males. The genetic possibility of all these expected events cannot be denied. There exists a case of a moth (*Nemeophila plantaginis*) where male dimorphism (without female dimorphism) exists. Unfortunately the genetics are not clear, though the few data available (some of my own) suggest a simple Mendelian difference. Further, in cases in which a considerable sexual difference exists, mutants occur which affect both sexes equally, others which affect only the male wings, others affecting female wings. Examples of all three types have been described in *Lymantria dispar* (review in Goldschmidt, 1934), and here recessive mutants as well as multiple alleles affecting different parts of the wing pattern have been found. Thus it remains a remarkable fact that sex-control of mimicry patterns is such a frequent occurrence. I cannot help feeling (and I have emphasized this before in Goldschmidt, 1913, 1920a, 1927) that there is a relation between the features of embryonic determination which makes for sex-controlled inheritance and the type of mutation (or saltation) which is involved in the production of the mimetic pattern. But this is a problem of developmental genetics, to which we shall return below.

E. Multiple effects

Both Fisher and Ford emphasize over and over again that the mimics differ from their non-mimetic males or their relatives not only in regard to wing pattern, but also in a series of other characters which are supposed to be part of the adaptation, but cannot be conceived as multiple effects of one mutant allele. Such characters exhibited in model and mimic are the form of the wings, especially the presence or absence of tails; the general ecology; the mode of flying; the presence of terminal knobs on the antennae and in palpi of the same color. Fisher considered the last characters so important that he devoted a colored plate to them. Such features, then, are considered as proof that the mimetic resemblance has been accumulated slowly by selection.

Let us begin with the tails. Nothing is known about the inheritance of tails in Lepidoptera. But we know (Süffert, 1929a) that in the development of the tails of swallowtails, first a normal wing edge is formed and secondarily cut out into the tailed shape by degeneration of peripheral parts. This fact makes the formation or nonformation of tails a rather simple embryological event, i.e., degeneration or no degeneration, which we may expect to find under simple genetic control. There exists one study of the genetics of wing-shape in Lepidoptera, that of Henke (1937) for the flour moth, in which lines with broader or more pointed wings exist. This shape, based upon differential growth, is already determined and visible at the time of pupation. Henke found that this growth is controlled by a single Mendelian pair *Pp* of which *P* mainly produces a shortening of the wing and a broadening and enlargement of the forewing. In *pp* the wingtip is more rounded. But here also a process comparable to that found by Süffert is encountered: the imaginal wing is not identical with the pupal wing, but part of its edge is cut out from the pupal wing by degeneration of peripheral parts (as described by Köhler, 1932). The allele *p* produces in the forewing a line of "cutting out" which is different from that in *P*; namely, a larger part of the pupal wing remains in regard to length, not in regard to breadth. Here, then, we see at work a type of developmental process comparable to that which produces tails in *Papilio*; in the flour moth this process is controlled by a single pair of alleles. One might add that in *Drosophila* single alleles are known which change wing shape in different ways, e.g., like the mutants expanded, the bran alleles of arc, and also certain loci like dumpy which produce changes of the wing edge (truncation) that closely resemble a formation of tails, including features of development (as studied by Auerbach, Goldschmidt, Waddington).

Also, an example from the Lepidoptera can be mentioned which involves sex-controlled inheritance, as was the case in the Papilios. The female and male of *Lymantria dispar* have wings of completely different form. The neo-Darwinian interpretation would be that a series of modifiers for these forms has been accumulated by selection, and some of these modifiers react only with the female, others only with the male genotype. But in intersexuality the typical shapes can be completely reversed. This happens at a definite grade of intersexuality; in intersexual females already in medium intersexuality, in intersexual males only in high intersexuality. There is no reason for advocating any modifiers if the facts can just as well be explained by one single genetic background with alternative reaction.

In the mimetic Papilios we actually face the following types:

1. *P. polytes:* Males and all three females with tails, also models with tails.
2. *P. dardanus:* Males with tails, females and models without tails, but one, *hippocoon*, sometimes with rudimentary tails.
3. *P. lysithous* (from Rio Grande de Sul; see Jordan, 1911), thus far not mentioned, with different females mimicking members of the Pharmacophagus group; three types of mimetic females with tails, two of the models tailed, one without tails.
4. *P. memnon:* Two non-mimetic females without tails like the male, but one mimetic female with tails like the model.

Thus we find perfectly good mimics with tails when the model is tailless, non-mimics with or without tails, males with or without tails, and females with and without tails whether mimics or not. An explanation, on Fisher's line of reasoning, requires different selections of modifiers for the presence or absence of tails, different reactions with the sexual genotype, and different reactions with the "switch genes." There is an additional need for an explanation in cases of incongruity between model and mimic. In view of the genetic facts indicating a simple control of wing shape, I prefer to assume that the different *A*, *B* mutants, the switch-genes, have multiple effects that either include or do not include the control of the tail-forming process in one or the other direction.

The second so-called multiple feature of the mimetic resemblance is the color of the pigment within the mimetic pattern. It is, in the cases which we are discussing here, a replacement of yellow by white or different reds or brownish. The genetics of a large number of comparable color varieties have been studied in Lepidoptera. Some are known to occur as simple mutants: Many red forms are known to produce simple Mendelian mutants of yellow color, red being dominant over yellow (e.g., *Callimorpha dominula* in N. Germany); yellow forms can produce purple mutants (in Arctiids); other yellows produce white mutants, with or without sex control (e.g., *Colias* with a female sex-control, or *Nemeophila plantaginis hospita* with male sex-control). But also simple Mendelian mutants are known in which the same color mutant affects also the pattern, e.g., the form *hospita* of *Nemeophila plantaginis* represents a change from reddish yellow to white simultaneously with a shift in the dark pattern. (For other examples see Standfuss, 1898, and Ford, 1937). One recessive mutant in the males of *Lymantria dispar* changes the ground color (not by a change in pigment but by the distribution of white and black scales) only in certain parts of the wing, thus changing the pattern. There is no genetic reason to assume that the pigments found in mimetic females differing from those of the males (and non-mimetic females) are the result of a slow selective process. It is certainly possible that they are based upon single mutations independent of the pattern. But there is no reason to deny that they might be just as well multiple effects of the same "switch-gene." Actually the data on intermediates agree well with this view (see below).

We turn now to the problem of color of the palpi and antennae-tips, though it is not involved in the cases of polymorphism which are in the foreground of the present discussion. The entomologist looks very closely, with a lens, at such small organs as are of taxonomic importance. But shall we really believe that birds, monkeys, or mantids distinguish such minutiae in a flying butterfly? If not, I cannot see how they could have been selected. In addition, what little we know genetically, does not point to an independent genetic determination of these characters as a basis of the assumed selection. It is known for a number of cases that the same mutant alleles in Lepidoptera control the color of different organs. Thus the yellow wing spot mutant of *Callimorpha dominula* has also a yellow striped abdomen, and in the melanistic combinations of the same moth the reduction of abdominal yellow runs parallel to that of wing yellow (photographs in Goldschmidt, 1924). In the melanistic varieties of the nun-moth the color of body hair changes parallel with that of the wings, and this includes also the hair tuft on the palpi (photographs in Goldschmidt, 1921). There can be no doubt that unifactorial control of wing and body pigment exists; therefore, there is no reason why the mutant controlling wing pattern and color should not also control color of palpi or other organs. One can exemplify also with the white and other alleles in *Drosophila*, which control simultaneously color of testis and Malpighian tubules; the same is true for the pale silver alleles (Goldschmidt, 1945).

The last of the so-called multiple mimetic adaptations are the ecological features like preference for the same habitat inhabited by the model, identical mode of flight in both (different from that of congeners), and similar observations. Aside from the fact that nothing is known of the genetics of such and comparable features, this group of assumed adaptations is to be considered as insufficiently established. In literature both pro and contra mimicry, statements of the most conflicting nature can be found, e.g., that the model flies in the plains and the mimic in the woods, or that the mode of flight of the mimic is so different from that of the model that even the dull human senses would not be deceived. Under these circumstances it is better to mark this group of doubtful adaptations as *non liquct.* It certainly is not fit to be used as a decisive argument in either sense.

F. Parallel geographic variation

It is a well-known fact that the models of mimetic forms, when widespread, have formed distinctive geographic races or subspecies, sometimes recognized as such, sometimes called species. If the mimic has the same range as the model it copies its typical local form. We mentioned above such cases in different mimetic species, especially in *Papilio dardanus.* Thus the female form *hippocoon* of West Africa is changed in the East into *hippocoonides* with a larger area of white in the hind wings; this is clearly an imitation of the eastern variety of the model *Amauris niavius dominicanus* (see Fig. 2). Many such cases are reported in the literature already quoted. But it must be added that geographic varieties of mimics are known for which no model exists. Ford quotes the case of *P. dardanus salaami,* in which in the eastern group all pale markings are orange, though no such model is available. In the western group the form *niobe* is a parallel orange variety, but here a model is present (*Bematistes sellus* Aur.).

Such facts of parallel geographic variation, again, are assumed to demonstrate the selection of modifiers in the origin of mimetic resemblance. Unfortunately, no genetic experiments of crossing geographic races seem available (except one reported by Ford, in which geographic difference was not represented). Thus we are completely left to analogies from other cases. The best analysed case of geographic variation in Lepidoptera is that of *Lymantria dispar.* Here patterns of the markings of caterpillars and, to a lesser extent, wing colors of the imago vary geographically. In both cases all or the major part of the differences are based upon systems of multiple alleles, i.e., mutants of the same alleles which in all races control pattern and color respectively. Apart from geographic variation, we know that frequently color variations and pattern variations are primarily based upon multiple alleles. Thus the complicated pattern of markings of the silk worm caterpillars is based upon a series of multiple alleles (many Japanese investigators, e.g., Tanaka). In the Tortricid moth *Acalla camariana*, the wing types brown marbled, black, and gray are controlled by multiple alleles (Fryer, 1928, 1931). The same is true for the melanic forms of *Aglia tau* L. studied by Standfuss (1910). It may be added that here ground color, pattern, and certain nail-like markings in the eyespots are involved in the multiple effects of the alleles. What is probably the largest series of multiple alleles controlling different patterns has been described in lady-beetles by Lus (1926). Thus I confidently expect that future research will reveal that the differences between geographic races of mimics (and models) will be of a multiple allelomorphic character, involving the locus controlling the mimetic pattern. I do not doubt that the neo-Darwinians would say in this case that in fact an allele of one of the supposed modifiers reacting with the switch-gene is responsible. Our answer to such an assumption is contained in the previous discussion.

There remains the problem why the subspecies of the mimic resemble the subspecies of the model. The neo-Darwinian would have to assume that each subspecie of the model was first formed as a pre-adaptation to the new habitat by one or another genetical process. The mimic, however, if entering the same region, was subjected to the selection of modifiers which changed its pattern towards resemblance to the new type of model. Let us discuss whether our knowledge of geographic variation warrants such assumptions.

The huge material on this subject has been recently reviewed from different points of view in the books by Dobzhansky, Mayr, Goldschmidt, and Huxley, where details and literature can be found. As we are discussing here a case in the Lepidoptera, we shall lean especially on material taken from this group. Though the adaptive nature of visible geographic variation is not always discernible, a sufficient number of cases has become known in which it has either been proven or is suggested that the visible differential characters, though themselves not adaptive, are the external visible effect of physiological differences which are of an adaptive nature. Many examples for Lepidoptera can be found in the present author's work on *Lymantria dispar*, and among them is at least one involving changes of pattern which might be easily compared with those described for the subspecies of *P. dardanus* (see discussion above). It has been known for a long time that characteristics of geographic races in different groups of animals and plants tend to run in a parallel series, e.g., northern races of different mammals and birds tend to be larger or darker, etc. These so-called rules, e.g., Bergmann's, Gloger's, and Allen's rules for vertebrates or Vavilov's for cultivated plants, have been fully discussed in the repeatedly mentioned books. There can be no doubt that wherever such rules are actually proven the important fact behind them is that in some way mutants of pigment, size, etc., are physiologically preadapted to definite habitats into which these forms are able to migrate. Preadaptation, selective migration of preadapted mutants into definite niches, and the similar physiological background of different but similar-looking mutants furnish the adequate explanation. In the Lepidoptera many examples of all this are known, although no "rules" have been laid down. We might quote the facts of industrial melanism already discussed above. This melanism occurs in such different families as the Geometridae, Lymantriidae, Tortricidae, and Saturnidae. The basic patterns of these groups and the species in question are rather different, and so are the intermediate steps, e.g., of the pepper moth and the nun moth. But the end product of this selection, black wings, is more or less identical in all. There is no reason to deny that similar potentialities are present in the families to which mimics and models belong. Actually Punnett has already discussed a good example. He mentioned the observation, made already by Bates, that in South America "certain color schemes are characteristic of distinct geographical regions . . . where they may occur in species belonging to very different genera and families" (l.c., p. 138) (Fig. 6). This local fashion[1], as one may call it, occurring in Heliconines, Ithomiines, Pierids, and Nymphalines has been claimed to unite simultaneously all these forms into a mimicry ring; but this is more than doubtful. Punnett pointed out, properly I think, and as far as I am aware, for the first time, that it

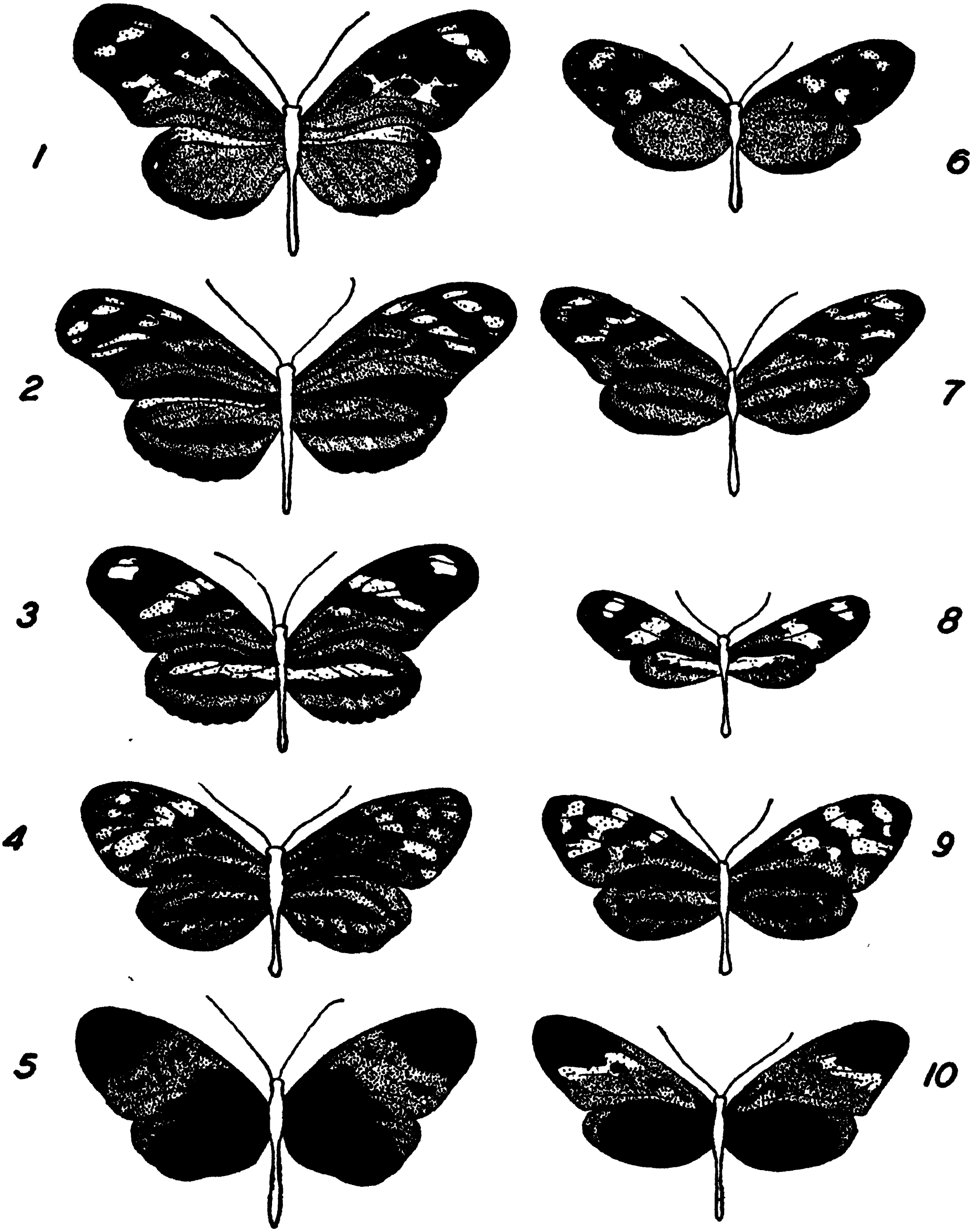

FIG. 6. GEOGRAPHICAL FASHIONS, EMBRACING DIFFERENT FORMS FROM PUNNETT, 1915, PLATE 15 IN COLORS, REDRAWN

Parallel series of patterns in Heliconinae and Ithomiinae.

1. *Heliconius mirus*
6. *Mechanitis elisa*
2. *H. telchinea*
7. *M. saturata*
} Central America

3. *H. eucrate*
8. *M. lysimnia*
} Eastern Brazil

4. *H. pardalinus*
9. *M. egaensis*
} Upper Amazon

5. *H. splendens*
10. *M. methona*
} Ecuador, Peru, Bolivia

is more probable that the local fashion is based upon some hidden physiological properties combined with definite patterns, i.e., the same interpretation which has been proven to be true in other cases (presented, e.g., in Goldschmidt, 1940).

Returning again to the parallel geographic variation of model and mimic we conclude that the explanation derived for comparable cases not involving mimicry should also cover the situation in mimicry. But this does not yet solve the genetical problem in the mimicry case. Again we can draw conclusions about this only from comparable cases, as there is no direct information available. The facts found in those cases point to either of two possibilities in the case of parallel geographic variation of mimics and models: either the appearance of simple sex-controlled mutants which are simultaneously under control of the "switch genes"; or of an allelic mutation of these "switch genes" themselves. As long as no proof to the contrary is available, I prefer the latter simpler solution. We shall see below that the facts concerning intermediates corroborate such conclusions.

G. *Parallel mutation*

The foregoing discussion leads directly to another problem, which is more or less intertwined with it. We reported above Punnett's theory of the origin of mimetic resemblance by parallel mutation of identical genes. A comparison was made with the parallel color mutations in different species of rodents. Today, one could also allude to the examples in cultivated plants described by Vavilov (1922). Both Fisher and Ford (l.c.) take exception to Punnett's conclusion. They point out that the similarity between model and mimic is only superficial. Though the pattern may appear very much alike in general, this effect is produced by different means. (This statement is not developed in detail for the Lepidoptera in question. I assume that these authors meant that, for example, in one species, a spot in the cubital cell may have the same general pattern effect as a spot in a different cell in the other, etc.) The pigments involved may be chemically different. In addition, Ford emphasizes what he believes to be a corollary (impossible, as he thinks) to the idea of parallel mutations, namely, that the differences between dissimilar and often not closely related species ought themselves to be unifactorial if copied by a mimic exhibiting unifactorial mimetism. I seriously doubt the logic of this "corollary."

For a discussion of this topic we ought to distinguish clearly between different types of mimicry. If a *Kallima* mimics a dry leaf, parallel mutations in model and mimic are certainly excluded. If a beetle mimics an ant by a specific optical effect of shading on the thorax, again parallel mutation is excluded. If a Pierine butterfly mimics an Ithomiine, parallel mutation, however, cannot be exluded. If different elements of the respective patterns are able to mutate so that a similar effect is produced in both forms (see the example of industrial melanism) we may call this parallel mutation, as seen from the angle of the phenotype. If the yellow pigment N mutates to red and so does the chemically different pigment M, this is parallel mutation as far as the phenotype is concerned. I agree that Punnett did not make a good point of his case in detail. If a corollary to the idea of parallel mutation would be that both forms have "the same genes," the case of Fisher and Ford would be a good one. But if parallel mutation is—as the physiological geneticist has to contend—the presence of a definite developmental system which permits only phenotypical changes of a definite type, the situation is completely different. (Simile: The river Meander and the river Seine have a similar phenotype (meandering) because the pattern of flow can be changed only in some definite ways by orographical conditions. But the hills and rocks of Asia Minor and France may be basically completely different and thus might be the chemical composition of the respective waters.) Whatever the mutating genes, the phenotypical changes have their prescribed pattern. This deliberation shows that the facts mentioned by Fisher and Ford in no way preclude parallel mutation between two species of Lepidoptera (see below, under pattern). Thus in such cases as the parallelism of Ithomiines and Pierids, where nothing is known of their genetics, but where non-mimetic Pierids are known which show a potentiality for Ithomiine-like pattern in the Pierid system of wing differentiation, parallel mutation, as understood here, cannot be excluded *a priori*. But this problem does not enter such situations as those in which unifactorial inheritance is known in the polymorphic mimic.

Let us take first the case of one *Papilio* mimicking another, specifically the *memnon* case, with two non-mimetic females, one of which resembles the male, and one mimetic female. According to Ford, few workers would be willing to accept the view that the model Pharmacophagus type *coon* has been derived from a *memnon*-like ancestor by a single mutation. We have mentioned already that there is no logical reason for this corollary. We do not know how the warning coloration of the model has been evolved; the fact (under dispute) that a similar type has been formed in a different species by a single mutation in no way gives information as to how the protected type originated. But I do not know of any reason why it should not have originated by a single mutation (we speak only of wing pattern). Actually, the pattern is not much different from that of other Papilios of the same general pattern group, certainly not more so than the patterns of the two non-mimetic females of *memnon* (which have not either been selected for pattern). Whatever the "genes" of the two *Papilio* species, the system of wing patterning available in the developing wings of the two species is such that changes in the same direction are possible, whatever the detailed procedure may be. This change may be brought about in one step in both species, or in one step here and many there, or in many steps in both, just as melanism can be one mutation or a set of additive ones. We might speak of a parallel mutation, in any case, but we must realize (what neither Punnett nor his opponents did) that parallelism does not mean the presence of "the same genes" or the same genetic history but of a similar developmental system which permits parallel changes to the same phenotype by many different genetic means. I might mention here, as I have on former occasions, the yellow mutant of the red-marked *Callimorpha dominula* and a geographic race of the same species in which the yellow is multifactorial. If both were to occur in the same locality, we would have a perfect example for the present discussion, except that both genetic types are here found in the same species.

The logical error in Ford's "corollary" becomes still more patent if we take the case of a mimetic female of a *Papilio* mimicking a Danaid or Acraeid. In my opinion, the unifactorial difference between one papilionid pattern and another mimetic one has no bearing whatsoever upon the genetic basis of the Danaine pattern. This might have originated in any conceivable way. It might be the ages-old pattern of the group, it might be the product of a slow or a fast evolution, or of direct evolution or one with whatsoever detour; all of which we do not know, as long as it is not possible to analyze this pattern by crossing experiments. But what has the origin of this pattern to do with the possibility that an existent pattern of a Papilionid may mutate into one of a type simulating that present in the Danaid? Clearly, then, the discussion of parallel mutation either does not make much sense, or else it amounts to a discussion of developmental potentialities, i.e., of the physiology of pattern formation. For illustration, I might return again to the model of melanism. We have discussed above the geographical "fashions" of South American butterflies of very different families, (Fig. 6) which included also parallel series of Heliconinae and Ithomiinae, a phenomenon which might or might not be connected with mimicry. Now it has been known that the same two groups may exhibit a parallel series of variations within the same locality (according to Kaye), which might be described as a kind of progressive melanism. One such case is illustrated in Fig. 7. But comparable series can also be found in other families and in another case described by Kaye, even in two species of the same family (Fig. 8). We can hardly err if we assume that, in the first case in both families and in the second in both species, the general features of the pattern system (namely, tendency to a barred pattern), whatever their genetic basis in either group, permit pattern changes which are necessarily parallel in both groups, because increase and union of dark bars will always look more or less alike. This shows clearly how we ought to look at so-called parallel mutation: not as geneticists but as embryologists.

We might, at this point, draw attention to a well known case of mimicry in plants, which Watkins mentions as a good parallel to animal mimicry and which makes a good case for properly understanding parallel mutation. The weed vetch, *Vicia sativa*, has been selected, clearly by the procedures of human agriculture, to resemble in many respects the lentil, *Ervum lens*, with which it is harvested, a case of parallel mutation, which could be discussed in the manner just applied to animal mimicry.

H. The intermediates and incompletes

We have described above the transitional forms found in different mimics, e.g., an intermediate form between the yellow and dark females of *P. turnus*, the intermediate females between two *Hypolimnas* forms and the different incompletes of

P. dardanus (see Table 4). In the *P. turnus-glaucus* case Ford speaks of incomplete dominance. But in the *Hypolimnas* example he insists that the reappearance of one intermediate together with two mimetic types in the offspring of an intermediate female (among eight females) is exactly what Fisher's theory requires. It seems that he draws the same conclusion from the existence of the incompletes in *P. dardanus*. He stresses the fact that these are usually rare, but are very frequent in a region where the model is missing, i.e. where selection ceases. The implication is that in the

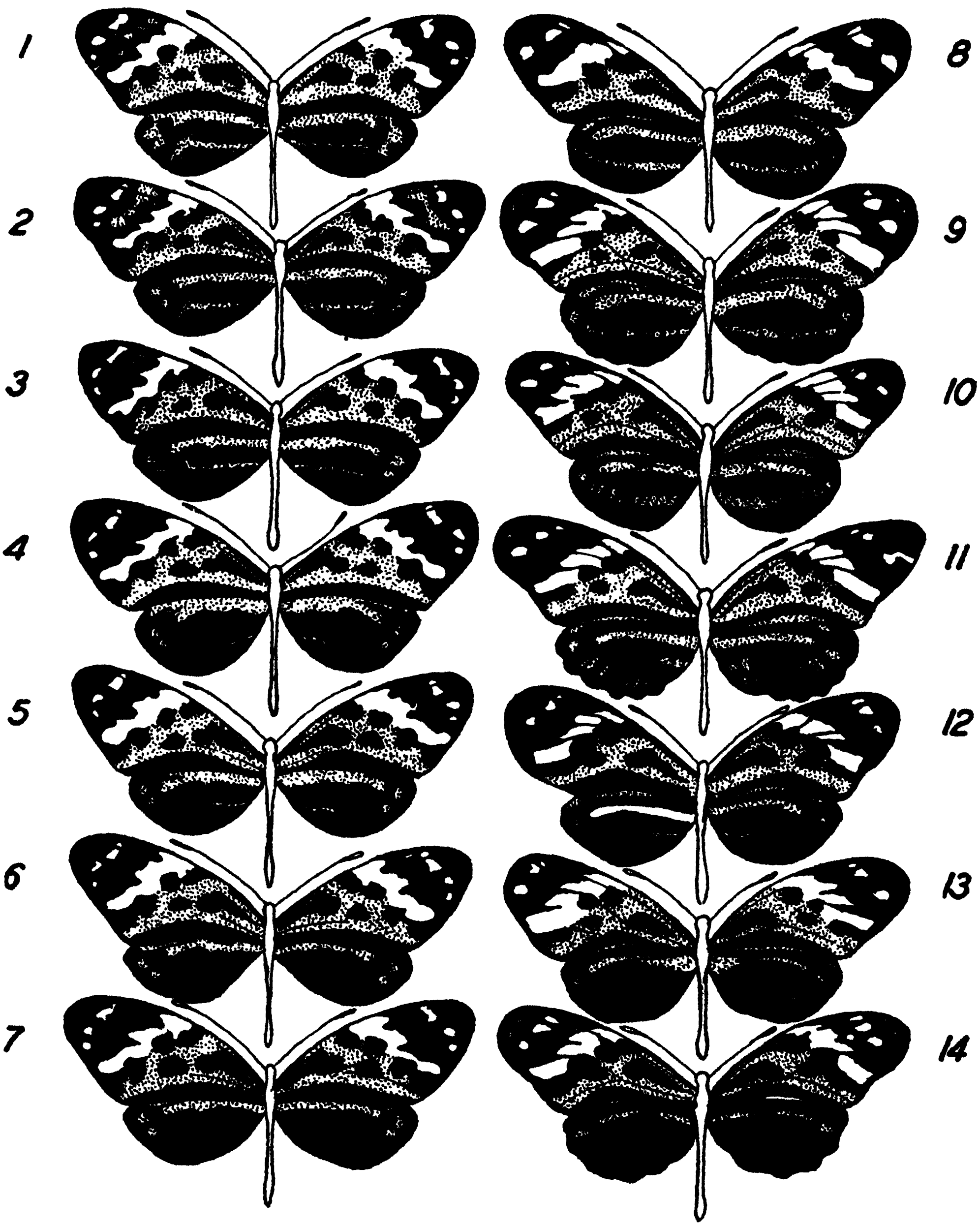

Fig. 7. Parallel Transitions from Barred to Black Hind Wings in an Ithomiine Butterfly Melinaea mneme (Left Row) and Its Heliconine Mimic Heliconius numata (Right Row), from the Potaro River, British Guiana

Redrawn from photographs by Kaye

absence of selection for mimicry the modifiers of the "switch gene" may mutate, or recombine differently, or revert towards the ancestral combination with impunity. (Ford does not mention which of these genetic possibilities he prefers; maybe all.) Thus we must look at the available facts to see whether they are not only in general agreement with the theory, but are even exactly what is expected, as Ford claims.

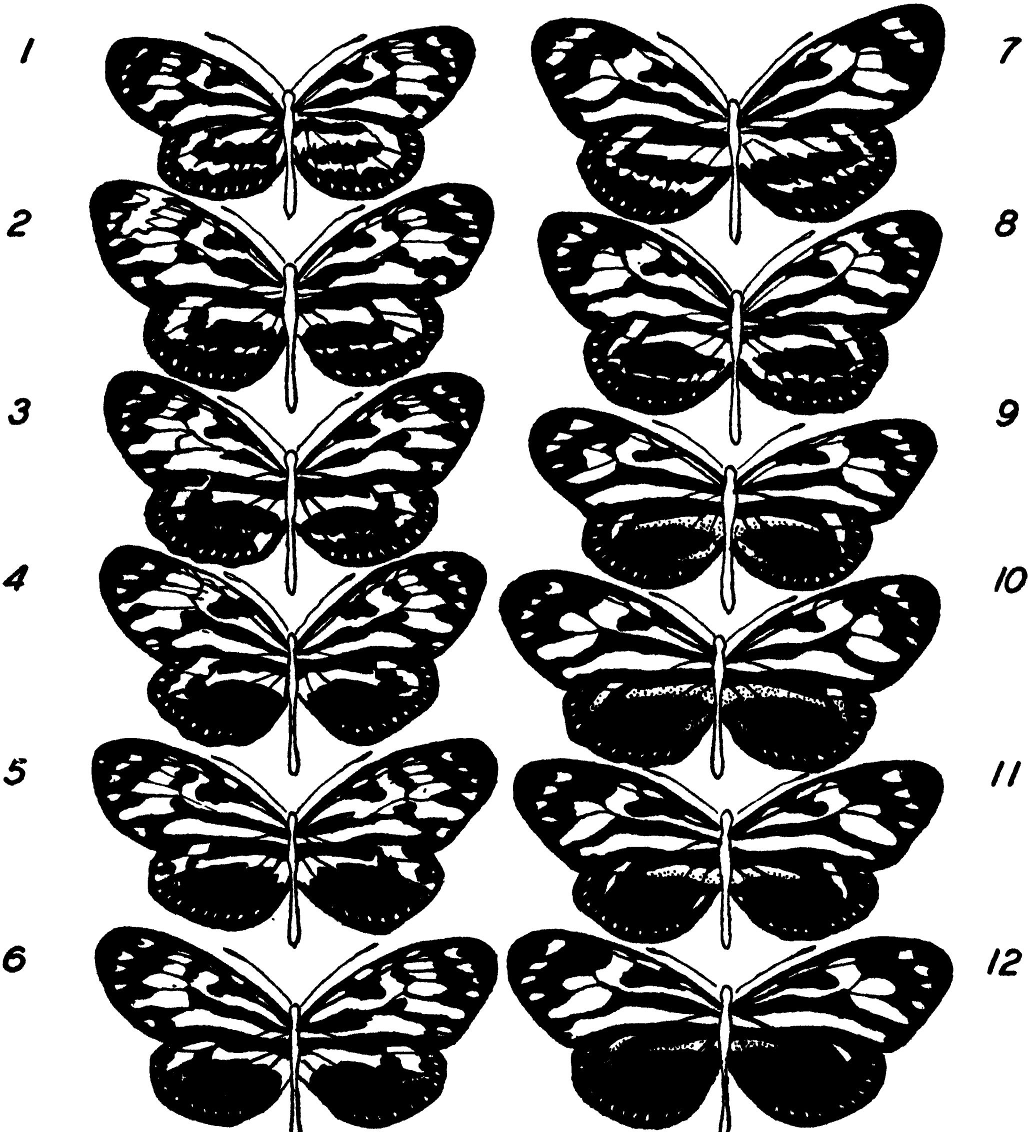

Fig. 8. Parallel Transition from Barred to Black Hind Wing in Two Lycoreane Butterflies, Lycorea pasinuntia, Left, L. ceres, Right, from the Potaro River, British Guiana
Redrawn from photographs by Kaye

Let us suppose that a system of the type demanded by Fisher's theory exists and that, with suspension of selection pressure, the modifiers behave in one or in all of the possible ways just outlined. Then the offspring of incompletes and intermediates ought to show a multiple factor segregation into many transitional types between the non-mimetic ancestral and the present form. Even with the numbers available in the families

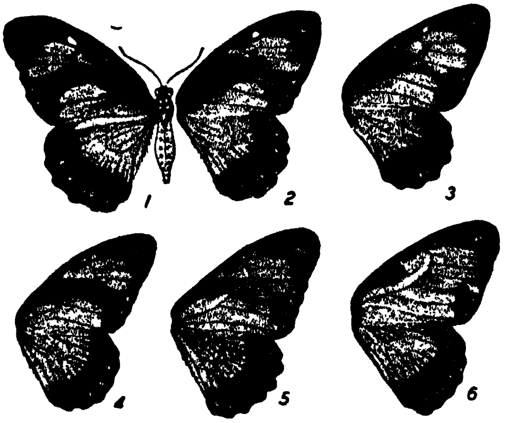

FIG. 9

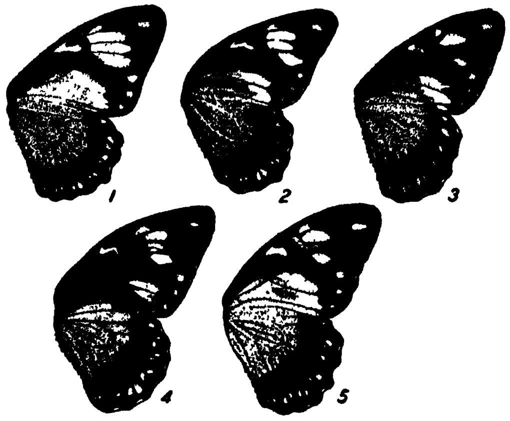

FIG. 10

FIG. 9. SERIES OF WINGS OF PAPILIO DARDANUS POLYTROPHUS BRED BY VAN SOMEREN

1 called *poultoni*, *4* called *proto-salaami*, *2* and *3* transitions towards *poultoni*, *5* transition to *dorippoides*, *6* *dorippoides*. Ground color brownish, yellow spots and patches of male yellow in ground. Redrawn from colored plate in Ford, 1936.

FIG. 10. P. POLYTROPHUS LAMBORNI (PROTOTROPHONIUS)

Variability of the intermediates; specimens partly captured (*5*) partly bred (the others). *1* is the type *lamborni*, *4* intermediate between *1* and *cenea*, others variants of *lamborni*.

Spots on both wings yellowish, ground color brownish, more or less small admixtures of male yellow (intermediate shading) are difficult to bring out in line drawings. Redrawn from colored pictures in Ford, 1936.

studied by Ford something of this kind ought to become visible. But Ford himself points out repeatedly how simple the segregation is in the offspring of incompletes, in some cases clearly a 1:1 ratio. There is only one result which might be claimed for multiple factor inheritance, and this is not concerned with the relation of mimic to non-mimic but with a small variability of one feature (dark band) within one of the incompletes. Actually, the incompletes reproduce either their own type, or their own type and the mimic, or two different mimics, or even two mimics and both their incompletes, in what looks like simple Mendelian ratios (although in many cases more than one mating is not excluded). I am unable to see how such results may be interpreted in Fisher's sense.

But is there any indication as to what the incompletes and intermediates are? In the case of *P. turnus*, Ford assumes that incomplete dominance is involved. The only reason I can see why this simple and obvious explanation is acceptable here, but not in the other cases, is that the difference between the two females of *turnus* appears to be small. In the *Hypolimnas* case, where intermediates between two mimetic females are found, the simple explanation of incomplete dominance with a certain amount of plus and minus variation is not invoked, though no reason can be found for discarding this simple explanation. A change in dominance may be due to the presence of a genetic dominance modifier or of a multiple allele with different dominance relations. Selection for or against dominance in Fisher's sense may be involved or not; selection for dominance, however, does not have anything to do with selection for pattern modifiers. I do not see any reason why the *Hypolimnas* case is not simply a problem of dominance within the unifactorial determination of alternative patterns. In another case, studied by Carpenter (1913) in *Pseudacraea eurytus*, the genetics are unknown, but no reason exists for assuming a different explanation except that, if more than one female form is involved, modification of dominance as well as of epistasis might be present. Again, a certain amount of variation, pictured by Carpenter, is in agreement with other known cases of modification of dominance, e.g., for the *vg*/+ heterozygote in *Drosophila* (see Goldschmidt, 1935).

In the case of *P. dardanus polytrophus*, however, something different enters the picture. Here the male has the yellow (fluorescent) dark-banded ancestral type with tails; the females are all mimics without tails and never have the basically different male pigment. The intermediates, however, have more or less of the male "ancestral" fluorescent pigment, more or less rudimentary tails, and more or less of the additional dark pigment which distinguishes the mimetic female from the male pattern. Such intermediates, and their range of variation, are pictured as well as it is possible without color, in Figs. 9 and 10 for the forms *protosalaami* and *prototrophonius*. In addition intermediates show a simple type of inheritance. If one looks upon such facts as a geneticist and especially as a physiological geneticist, i.e., without any reference to theories of evolution, only one interpretation seems possible. The intermediates are the product of incomplete sex control on a genetic basis. The genetic basis may be a mutant shifting the process of sex-controlled inheritance more or less beyond the threshold or it may be a multiple allele of the pattern factor which happens to entail a less perfectly working sex-control.

If we want to visualize the workings of such a situation in the determination of the sexual pattern it does not matter very much which of the eventually possible interpretations of sex-control we assume, that presented by the present writer (Goldschmidt, 1927), or any other not yet proposed. In a general way sex-control must always mean that the developmental patterning processes are proceeding in such a way that different thresholds for the action of the pattern factors exist in the two sexes, and this in an all or nothing set-up. Any environmental or genetic agency which affects this threshold condition may shift the sex-control partly or completely by disrupting the all or none reaction. (Excellent material for the demonstration of this viewpoint can be found in the behavior of sex-controlled characters in intersexuality, as discussed at many points in my books of 1927 and 1938. Actually one might call the *Papilio* intermediates wing-pattern-intersexes). It would be easy to develop specific ideas on this subject. But the main point is the general principle which, to me, seems obvious and in harmony with the facts.

A powerful argument in favor of our interpretation can be derived from a group of, I think, misrepresented facts recorded by Poulton. Already in 1906 (Plate 18) Poulton had pictured what he called a gynandromorph of *P. dardanus planemoides* with male spots on the left wings. Later he reported in detail (1927) on a group of eight gynandromorphs, which it is claimed were produced experimentally by dropping young pupae. I have discussed the facts already in my book on sex-intergrades (1929a) and I have shown that the interpretation must be wrong except for one specimen which is clearly a gynander, probably obtained by chance. Fig. 11 presents outline drawings of some of the specimens which, however, fail to show the male yellow pigment. Three of the others are *hippocoon* females with some splashes of male yellow color and more or less of tails. The genitals are female. Four are clearly males. One has a few patches of *hippocoon* female admixture; one has more such admixture on one hind wing, together with absence of the tail; another one is a male with scattered black female streaks on the fore wings; the fourth male has, on the left fore wing, scattered female *hippocoon* parts, while both right wings show the general female *hippocoon* pattern but with the addition of male patches.

Without discussing the claimed origin of these freaks by a tactile shock (which is not impossible if the shock occurred during the sensitive period) we may say with certainty, in view of our knowledge of gynandromorphism in Lepidoptera, that this phenomenon is excluded (see Goldschmidt, 1929a, p. 472 ff.). In my opinion the proper explanation is that in the males in question the mechanism of sex-controlled inheritance was somehow wrecked in part, so that here and there on the wing the dominant pattern of the other sex became visible. The females, however, should be explained exactly as has been done above for other "intermediate" females. This, then, seems to be the genetical situation for the incompletes. It is in no way opposed to Carpenter and Ford's explanation of the *distribution* of intermediates as a consequence of cessation of selective value for the mimetic pattern. But I believe I have shown that this selection has nothing whatsoever to do with the *origin* of mimetic patterns.

1. Pattern determination as basis of the problem

We have mentioned repeatedly that certain points under discussion required a solution from the standpoint of developmental physiology. The basic idea of the Fisher school is that it is impossible to imagine that the complicated pattern of mimetic resemblance could have been produced in one mutational step. It is clear that an objective analysis of this problem requires a knowledge of genetics and development of the wing pattern of Lepidoptera. Such information in regard to its actually known potentialities would permit conclusions concerning the possibility or impossibility of pattern changes of considerable magnitude. There is unfortunately no embryological (including postlarval development) and no experimental work on the present subject available for mimetic forms. But we know something about pattern development in other Papilionids (Goldschmidt, 1923, for *Thais polyxena*) and a good deal on other different aspects of the problem for a number of groups of butterflies and moths, including families which have furnished examples of mimicry (Nymphalines). A study of such facts, as far as they have a bearing on our present problem, will have to embrace the subjects: general rules of wing pattern, experimental shift within the pattern, potentiality of shifts without genetic change, the known types of genetic change, and the potentialities of change as derived from all other sources of information.

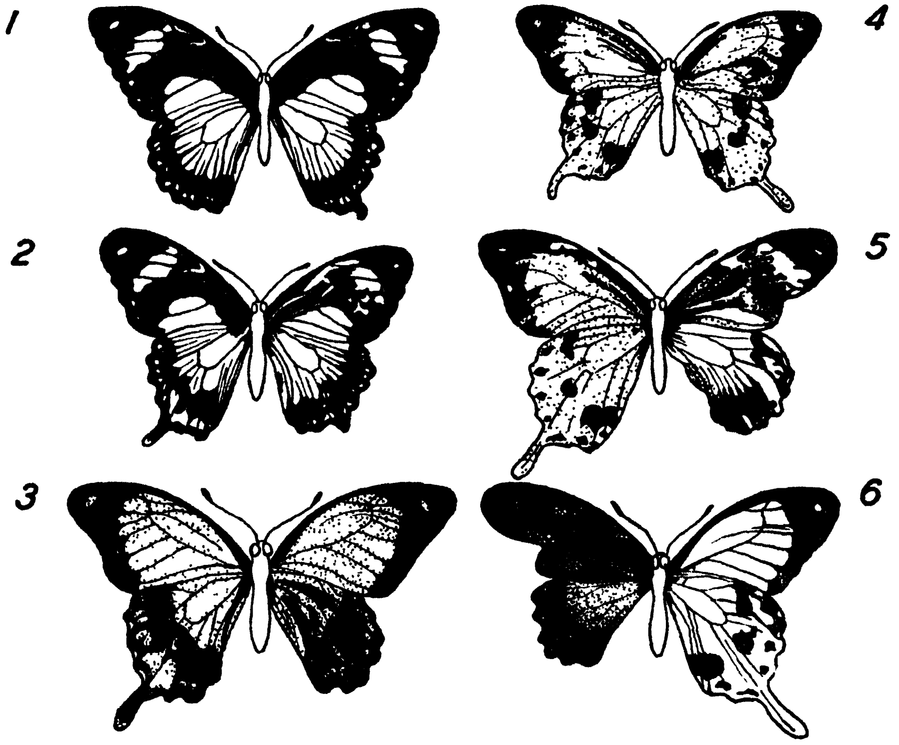

Fig. 11. A Series of Poulton's So-called Gynanders; Only *6* Is a Real Gynander, Left ♀, Right ♂
Notice more or less rudimentary tails in intermediates. Splashes of male yellow scales do not show in the drawing, after an uncolored photograph by Poulton.

1. Comparative morphology of the wing pattern

A long time ago Eimer (1897), in his famous work on orthogenesis, tried to find rules governing the wing pattern of Lepidoptera. But only in recent times have Schwanwitsch (1924 ff.) and Suffert (1927 ff.) discovered independently what may be considered a general rule. There are a number of features in the patterns of both butterflies and moths which are of a more general nature: pigment may be deposited upon the wing veins and also upon the tracheae not enclosed in veins (extreme example—some tropical Pierids); pigment may also be deposited in stripes between the longitudinal veins (extreme example—some of the Asiatic Papilionids studied above); a ground pigment (also optical colors, e.g. *Morpho*) may cover the entire wing between whatever pattern is present (e.g., whites without much pattern, monarch butterfly with ground color between pattern); a ground pigment may cover only parts between the pattern elements, or more than one color may cover different cells or groups of cells either in both wings, or in only the fore or hind wings (examples—the colorful admirals and underwings, and most tropical butterflies like the gorgeous Ornithopterae). All these general pattern types enter also the different mimetic patterns. In addition, the pigments in the patches may be chemically different, e.g., pierin, pteridin, different flavones; white may also be the optical effect of air-filled scales.

Aside from these generalized pattern elements there exists a special pattern of crossbands which basically is more or less alike in all groups, though it may be suppressed, enriched, or distorted in individual groups. The basic type of this pattern was discovered both by Schwanwitsch and Süffert and corroborated by others who studied different groups of Lepidoptera (e.g., Kühn, Henke). Fig. 12 illustrates this basic pattern, following Suffert's terminology. In the center is the central system of symmetrical bands Cd and Cp around the discoidal spot (D). Proximally from this the "hollow band" H is found, so-called because it frequently looks like a bowl with reenforced edges. Still more proximally follows the root band (W). H, W, and D tend to have a similar structure and are called the hollow elements. Distally there is a second symmetrical system, the ocellar system, with the symmetrical bands Op and Od with the ocelli in between. Two marginal bands, R_1 and R_2, follow the wing edge. It is remarkable how a great many different patterns may be derived from this basic one by splitting, fusion, disappearance, shortening, simplification or complication, and shifting of the main elements, processes in which the different systems (both symmetry systems, hollow elements, marginal bands) tend to vary independently. We need not go into details but point to the monograph of Henke (1936) in which this has been carried out in much detail for all important types of the Saturnid family. In the Papilionids, likewise, this sytem is the primitive one. It is still found in our *Papilio turnus* (which has a mimetic female *glaucus*, see Fig. 1). The actual pattern is produced here by a shift which makes some of the bands unite with parts of other bands, as Fig. 13 from another type of Papilionid illustrates. (In the mimetic form *glaucus*, by the way, all bands of the forewing have been reduced to shadows together with the appearance of dark ground color; see Fig. 1. It would be difficult to claim that this could not be accomplished by one mutant.) In some of the mimetic species of *Papilio* the system of bands has completely disappeared on the forewings and has also been considerably modified on the hind wings (e.g., *memnon*). In others, e.g., *polytes*, the system is completely covered in one form, partly visible in another, and better developed, though thoroughly modified, in the third. In the *dardanus* case, the system is rudimentary in the normal form and relatively little changed in the mimetic wings except for a change in general appearance and the fusion of some of the elements. The pattern of the models has exactly the same basis in so far as the relation to the primary bands is concerned.

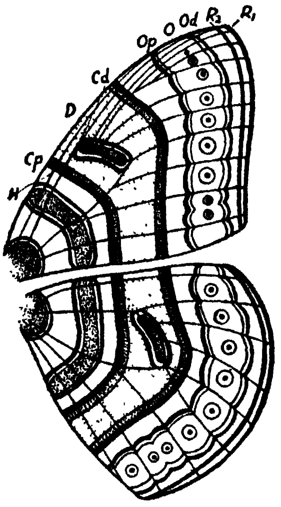

FIG 12. SÜFFERT'S DIAGRAM OF THE BASIC PATTERN OF THE NYMPHALINE WING; EXPLANATION IN TEXT

2. Development of pattern

If we want to understand the potentialities of the wing pattern in regard to major shifts produced by a single causative agent, we must be acquainted with the development of pattern. Though the work on this topic is far from complete, we know at least some decisive points. These can be grouped in four classes, leaving out of discussion special features, such as relation to veins and sinuses. (A more detailed discussion and special literature may be found in my book, "Physiological Genetics".)

1. The location of the bands on the wing can already be demonstrated in undifferentiated wings. According to the school of Kühn, mitoses are frequent only along the path of later bands, i.e., a mitotic pattern is a pre-

cursor to the later visible pattern (see Kühn and Henke, 1929–1936).

2. At a later stage, but before any color appears, the pattern of the bands is completely differentiated. Goldschmidt (1920c, 1923) and students, e.g., Braun, found that the scales in the later dark bands of the pattern are soft and filled with blood at a time when those between the bands are already hard and finished. Thus a ghost pattern is produced which is based upon different speeds of differentiation in different sections of the pupal wing. The relation to the features of class one is that the mother cells of later dark scales in the bands have not yet finished multiplication and have not yet entered the phase of differentiation when the scales in between have already progressed considerably on the path of differentiation into scales.
3. In some cases (though not always) there is a relation between the shapes of scales and the pigment they receive (Kuhn and students, see Kuhn and Henke, 1929-1936).
4. The actual pigment does not appear simultaneously in the pattern but in a definite seriation. This applies to the pigment in the bands as well as to spots of a different color. (Work of Van Bemmelen, von Linden, a.o., literature in Biedermann, 1912.) Thus in one case studied by me (Goldschmidt, 1923) red spots on the hind wings of *Thais polyxena* were already pigmented while the rest of the wing still showed the ghost pattern; in addition the scales of these spots were completely finished.

Thus the main general features of pattern development consist in differential speed of growth and differentiation, and in a proper timing therewith of either the pigment forming reactions, or the local availability of chromogens and oxidase, or the readiness of the chitin of the scales to imbibe these pigments. (This system can best be presented in curves of reactions and threshold conditions such as are to be found in my book of 1927.) This very general review already indicates that genetic changes (mutants) may act upon minor details if their effect takes place late, but may change the whole outlay of the pattern if they act early in differentiation (differentiation meaning the actual determining processes which usually occur before visible differentiation).

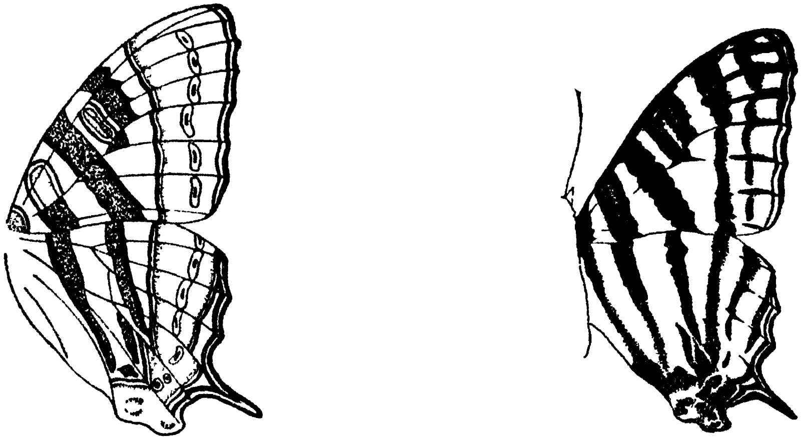

FIG. 13 WINGS OF CYRESTIS CAMILLUS, WITH A PATTERN COMPARABLE TO THAT OF PRIMITIVE PAPILIOS BUT EASIER TO ANALYZE (RIGHT)

Left, its interpretation in terms of the basic pattern elements. Redrawn after Suffert

3. Experimental shift of pattern

The potentiality of pattern changes in a given wing can best be tested by non-genetic experimentation that uses simple and known agents. A very large body of facts has been collected, which may be summarized shortly under a few headings.

1. The pattern may be shifted by action of environmental changes upon the early undifferentiated wing (The immense body of earlier work by Weismann, Standfuss, Merrifield, Fischer, von Linden, *et al.*, is minutely reviewed in Biedermann's monograph, 1912. For more recent work

by Federley, Kosminsky, Goldschmidt, and mainly by Süffert, and Kühn and his school, see the review in Goldschmidt, 1938a, and more recent papers by Kühn and Henke and Kühn and Engelhardt, 1936.) The classical temperature experiments with moderate heat or cold, and with heat or cold shocks, as well as experiments with CO_2, chloroform, etc., have shown that the imaginal wing pattern can be considerably changed by treatment of the pupal wing at a time before determination, the sensitive (or thermolabile) periods. The effects are: changes in ground-color, expansion or constriction of spots, union of spots and bands, disappearance of pattern elements or haziness of others, dissolution of eye spots into the constituent bands, disappearance of sexual dimorphism, and production of transparent wings with change of shape of the scales. Many of these individual features resemble those found in different species and certainly also the *type* of pattern changes (not the details) present in mimetic forms. (No experiments with mimics are known; they would be very important; see above, however, the discussion of Poulton and Van Someren's so-called gynandromorphs.) In some cases the experiment produces an exact copy of a geographical race of the form subjected to the shocks, a so-called phenocopy. Certainly the potentialities of patterning are considerable, and very different patterns may be realized by influencing the basic developmental processes.

In some of these experiments, Kuhn (and students) found an additional important fact (see especially Kuhn, 1926; Kuhn and Engelhardt, 1936). The different pattern elements, e.g., the symmetry system, the marginal bands, etc., have different sensitive periods in which they can be influenced by environmental agencies. Thus, as a rule, the pattern does not react as a unit if the treatment is fractional, but will act as a unit if the treatment covers the whole period of sensitivity. In detail, the sensitive periods occur at different stages of development in different species (e.g., flour moth and *Abraxas*). They may be different for fore and hind wings, and also different reactions to cold and heat have been found.

Still more important are the experiments performed by Kuhn and students on the flour moth, and by Henke on Saturnids (full review and literature in Goldschmidt, 1938a). They succeeded in inducing considerable shifts in the pattern by destroying (by heat) parts of the larval wing before the primary patterning processes take place. As the members of some of the systems of bands, e.g., the symmetry system, were found to be determined at the edges of a spreading stream of determination, an interference with this stream dislocates the bands correspondingly. The effect was a completely unusual pattern very different from the normal arrangement of bands. Generally speaking, this whole group of experiments indicates that very simple agencies, like blocking the path of patterning processes or shifting the time elements involved in these processes, may produce very different patterns in regard to small details such as size and color (and also structure, when optical colors are involved) of spots, or development of scales, as well as in regard to the primary pattern of the species, namely, the specific features of the bands and their derivatives

3. A special case of experimentation on pattern which is of paramount importance for the analysis of our problem is the work on seasonal dimorphism. Weismann had already realized its importance for the understanding of evolution and had performed classic experiments. The basic fact is that one and the same species shows in different generations different wing patterns which, in some cases, combine with completely different shapes of the wings. Thus, spring and fall types or dry and wet season types may be found In some of the cases the wing pattern differences between the two forms are small. In other cases they are large, even so large that the two forms have been described as different species. In such cases, the two types of pattern (and also shape) are quantitatively at least as different as the patterns of the polymorphic mimetic females of our present discussion. The only form experimented upon is that of the European *Araschnia levana-prorsa*, which is characterized by a rather considerable difference between the seasonal patterns. But the most extreme types have been described from tropical countries, such as *Prioneris watsoni-thestylis* from India, or *Precisoctavia natalensis* and *sesamus* from S. Africa. In Fig. 14 it is attempted to convey an idea of the differences in a black and white sketch. Temperature experiments (in *Araschnia*), initiated by Weismann, have shown that treatment of pupae in sensitive periods permits the production of all intermediates between the two patterns. (Good original photos of such a series in Goldschmidt, 1929b.) Süffert (1927) found later that one of the decisive features in determining the pattern differences is the presence or absence of a diapause. The details

do not belong here. The decisive fact for the discussion of our main problem is this: if a definite genetic situation is present in a species, a simple developmental mechanism involving a time element (retardation or speeding up of some reactions by temperature action or onset of diapause) can shift one pattern as a whole into a completely different one. In the case of proper experimental conditions the shift may be gradual, with all intermediate types. All this includes also some chemical differences (different colors), as well as shape of wings. Here, then, we have the visible differences of saltational magnitude, and also all grades of intermediates based upon one and the same genetical background but under different environment. Here certainly no room is left for combinations of modifiers. The application to the mimicry case appears obvious.

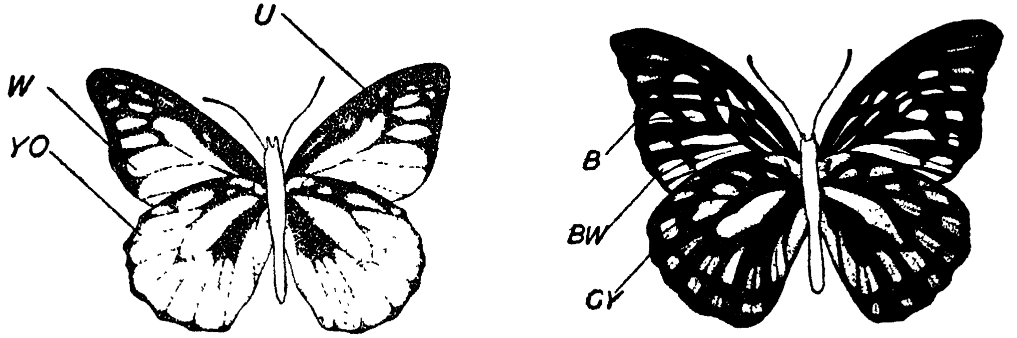

FIG. 14. THE TWO SEASONAL DIMORPHIC FORMS OF PRIONERIS WATSONI THESTYLIS FROM INDIA (UNDERSIDE) AND OF PRECISOCTAVIA NATALENSIS SESAMUS FROM AFRICA

Colors U, umber; W, white, Yo, ochre, B, black; BW, bluish white; CY, chrome Redrawn from a colored plate, after Doflein

4. Genetics of pattern

We have demonstrated the existence of a potentiality for smaller or larger, localized or all-inclusive changes of wing pattern within the same genotype. These can be brought to realization by different but simple natural or experimental influences at the time of pattern formation. Now we must inquire whether simple genetic changes, i.e., one step mutations, can have similar effects. *A priori,* we must expect that all pattern changes which can be induced by environmental agencies should also occur as the effects of simple mutants. This conclusion is derived from the work of the present author (1929a, 1935) and his followers on phenocopies (see review in Goldschmidt, 1938a and 1940; a very detailed and careful repetition of my *Drosophila* work, with mostly identical results, has been published since by Henke and collaborators, 1941). The experiments show that the phenotypes of practically all known morphological mutants in *Drosophila* (and some in Lepidoptera) can be copied as modifications produced by experimental stimuli. Actually our knowledge of pattern mutants in Lepidoptera is not so complete as desired, one of the reasons being that only few groups have lent themselves to experimental breeding on a sufficiently large scale. A great part of the material is reviewed in Ford (1937) Most of the cases involve inheritance of such simple differences as ground color of the wing. red vs. yellow, both vs. white, black vs. light, i.e., the different groups of melanism, rutilism, leucism, etc. Sometimes the differences are unifactorial, sometimes multiple allelic, sometimes additive factors or modifiers are known; in addition autosomal, sex-linked or sex-controlled inheritance may be encountered A number of these examples, in which elements other than simple color differences were involved, have been discussed above. Thus the phenotypic difference between *Abraxas grossulariata* and *A lacticolor* (now called *dohrnii* Konig), the classic example of sex-linked inheritance, is not simply described as the paleness of *lacticolor*, but actually a reduction of all elements of the primary wing pattern, bands and spots, is visible. In the same form and in many others the reciprocal process, frequently included in the term melanism, is known, namely, expansion and confluence of the pattern elements, involving the entire pattern. In *Lymantria monacha* mutant alleles are known which produce such an effect upon the pattern as a whole, while another mutant increases the pigment between the bands, i.e., the ground color.

Besides these generalized pattern mutants, which are usually included in the general classes of melanism and leucism (though some entomologists distinguish nigrism from melanism), a number of specific pattern mutants are known that influence definite single elements or a group of them (elements in the sense of the Suffert-Schwanwitsch scheme). The two species in which a relatively large number of such mutants are known are the flour moth *Ephestia kuhniella* and the gypsy moth *Lymantria dispar.* In the flour moth a number of mutants have been found (by Kühn and students) which do not affect the pattern as a whole but affect the different pattern elements individually (pictures in Kuhn and Henke, 1929, 1936). Thus mutants have been found which darken only certain bands or spots, others which affect different ones. But there are in addition mutants which affect the general coloring of the wing by increasing the breadth of all bands simultaneously, except the marginal spots. The most interesting mutants are those which affect the position on the wing of the bands of the central symmetry system, i.e., the same bands which could be shifted in the burning experiments (as reported above). One recessive mutant can pull these bands apart, another brings them together, conditions which entail a major pattern change. In *Lymantria dispar*, mutants are known (pictures in Goldschmidt, 1934) which affect the whole pattern in the same way as is typical for other melanistic varieties. In addition, mutants occur which affect definite parts of the pattern; one which changes the discoidal spots, or one which removes all bands except the marginal one. This is a rather large departure, as the zigzag bands are an important feature of the species. Still more extreme, in some ways, is a mutant which makes male wings almost white except for a dark rim, and simultaneously produces dark wing tips. This mutant is remarkable because it changes simultaneously the whole "costume" of the wing from one of uniform color, with the zigzag bands in the background, to one with a conspicuous pattern of differently shaded areas. These examples may suffice.

5. Application to the problem of mimicry

The facts of pattern determination in the Lepidopteran wing have been reviewed with the intention of proving that Punnett's theory of the origin of mimetic resemblance by saltation is in agreement with the known facts of pattern morphology, development, and genetics. The more general aspect of this conclusion can best be realized when we start from the phenomenon of seasonal dimorphism. Only few species of butterflies exhibit a considerable seasonal dimorphism with completely different patterns, though all Lepidoptera studied are liable to undergo more or less considerable pattern changes under experimental conditions. This means that the genetic background of the dimorphic species must, in a general way, control a type of development of wing pattern which is more easily shifted out of its typical sequence of events than is ordinarily the case. We do not have much knowledge of what this means in concrete terms. We know that the developmental processes can be affected only at a definite time, and we know that graded external factors can produce a graded effect. We further know that the normal controlling agent is the diapause, which entails a definite change in the velocity of all metabolic and developmental processes. Altogether, then, the genetic basis of pattern formation which exhibits the alternative form of reaction must control a set of interwoven developmental processes which are timed in such a way that they can be easily shifted into another gear. (I think that the best way of visualizing such a combination of reactions is by the diagrammatic systems of curves and threshold conditions which I presented in a simpler form in Goldschmidt, 1920a, and more elaborately in my book of 1927.) Whatever the details, the decisive fact remains that the potentialities for patterning have a very wide range which is contained in the genetic constitution, and that different agencies of a rather simple type can choose between realization of one or the other of the potencies just as we can make a definite tune be played by a "juke-box" by shifting one lever.

In my opinion, the origin of the mimetic pattern requires a similar genetic situation. The ancestral form must have had a type of pattern determination parallel to that present in seasonal dimorphic forms. This means a developmental system which can be switched into a very different one by one simple lever: in this case a mutation. The mutant must be such as to affect the *primary* patterning processes; it can change the pattern thoroughly because the proper developmental system is already available. Small wonder therefore that mimetism is about as rare as extreme seasonal dimorphism, and that it is confined to a few nearly related members of a few systematic groups (see above). I cannot see how such conclusions could be avoided in the face of the reported facts.

There is unfortunately no experimental evidence available of temperature, etc., action on mimetic forms and their non-mimetic relatives except the crude one of Van Someren discussed above. Such experiments performed on the non-mimetic (*meriones*), mimetic (*dardanus*), and variable races (*polytrophus*) of *Papilio dardanus* would be of supreme interest and might yield surprising results.

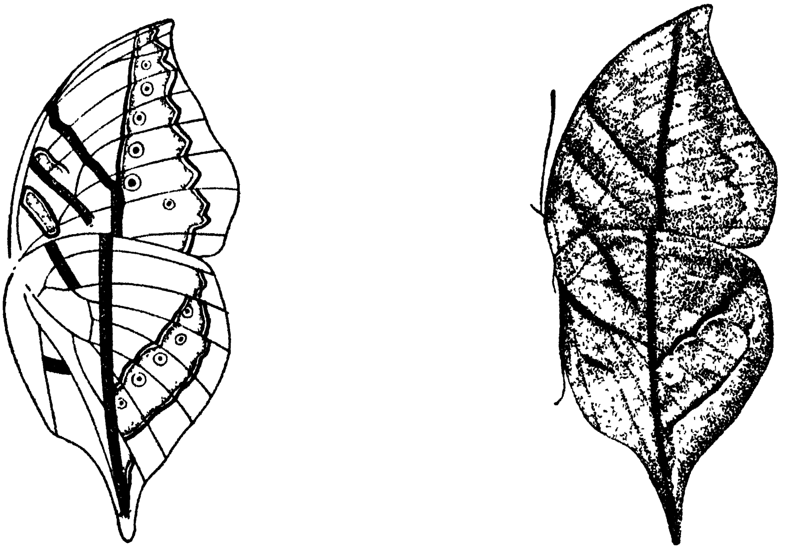

Fig. 15. Wings of the Leaf Butterfly Kallima inachis (Right) with an Interpretation in Terms of the Basic Pattern (Left). Redrawn after Suffert

But some points may already be visualized by an inspection of the pattern of the mimetic and non-mimetic types (see Fig. 2). The non-mimetic forms show a large expanse of ground color with complete reduction of most bands (less so in the hind wings), but a union of the marginal bands into a broad margin. In all mimetic forms one main character of the fore wings is the presence of the anterior sections of the proximal bands and their gradual union with the margin, which leaves islands of ground color (with changes of pigment) as spots and patches in between. In the most extreme forms all of the wing, except a few islands, is covered with the dark pigment of the expanded bands. In some cases the bands near the root of the wing take part, partly or completely, in the process. From our previous knowledge of pattern we know that these types are not different in principle from the different types of intermediates produced in seasonal dimorphic forms. The same holds for the different types of pattern produced by pattern intensification mutants in other forms. The bands which reappear under the influence of the mutant are obviously the ancestral bands of the group for which the potentiality is always present, just as the potentiality for wild type plumage is present in a white fowl. (The comparison is not meant to be genetic in detail.) The situation is simpler for the hind wings, in so far as the union of marginal bands, which is only a small step away from the non-mimetic form, constitutes a rather simple change (in addition to the change in color of the ground pigment). But in the hind wings (also in the fore wings in some forms) another pattern element frequently appears: the pigmented longitudinal bars in the center of the long wing cells between the veins. This is a pattern element for which the potentiality is generally present in the Papilio group. Actually it is the most prominent feature of the pattern of the Asiatic swallowtails. It is hardly necessary to continue to enumerate and to analyze other cases in detail. We think that it is clear that we are dealing with processes which an experimental embryologist might call the evocation of developmental potencies by the action of a mutant with the point of attack at the primary processes of pattern differentiation.

I might add that the foregoing analysis is, in many respects, a detailed elaboration of a short and general presentation of the subject in my book on the quantitative theory of heredity (1927). I find that an Australian entomologist, Nicholson (1927), has hinted at a nearly related viewpoint, not mentioning details of physiological genetics and development. He compared the pattern change in a mimetic pattern to the change of a picture when observed in blue light. A change of metabolism, he thought, might produce the whole pattern change, e.g., if the pigment is deposited earlier than usual. If he had been acquainted with the work on pattern formation and certain aspects of physiological genetics, he might have arrived at the same conclusions as are presented here.

It would be interesting to apply the same argumentation to other types of mimicry not under discussion here. I might submit Suffert's interpretation of the wing pattern of *Kallima* in Fig. 15 in terms of the basic pattern (see Fig. 12). This indicates to me that a single change in the growth pattern of the wing after the determination of the location of the bands will suffice to break up and reunite the bands in such a way that the major part of the leaf mimicry is accomplished at once. I might also point out that the same applies to any mutant whatsoever that influences early embryonic, i.e., patterning, processes. But this latter point has been sufficiently stressed in a recent book (Goldschmidt, 1940).

CONCLUSION

After reporting and discussing the significant facts, we came to the conclusion that Punnett's interpretation of mimetic polymorphism by mutation (saltation) agrees better with the facts than Fisher's neo-Darwinian theory. We have tried to prove this by scrutinizing in every detail both the logic and the factual basis of the controversial theories discussed by the former authors, as well as by studying many other aspects not discussed before. Among the facts pertaining to the situation under scrutiny we have given equal weight to those taken from the fields of genetics and evolution and to those of an embryological character. Such an all-round analysis has shown neither any need for the application of the more complicated explanation of the neo-Darwinists, nor any reason for abandoning the simpler solution, which fits all the known facts.

LIST OF LITERATURE

BAUR, E. 1911. *Einfuhrung in die Vererbungslehre* Berlin: Gebr. Bornträger.

BIEDERMANN, W. 1912 Farbe und Zeichnung der Insecten. *Hb. vergl. Physiol.*, 3 1657 1994

BRAUN, W. 1939. Contributions to the study of development of wing patterns in Lepidoptera. *Biol. Bull.*, 76: 226–240.

CARPENTER, G. D. H. 1913 *Pseudacraea eurytus* Neave, its forms and its models on Bugalla Island, Lake Victoria, with other members of the same combination. *Trans. Ent. Soc. Lond*, 1913· 606–645.

——. 1919. *Pseudacraea boisduvali* Doubl and its models, with especial reference to Bugalla Island. *Trans Ent. Soc Lond.*, 1919 646 655.

——. 1932. Mimicry. *Sci. Progr.*, 26 609–625.

——. 1937. Mimicry as viewed by Professor Shull *Science*, 85: 356–359; 86. 157.

——, and FORD, E. B. 1933. *Mimicry*. London: (Not seen; cited from Ford, 1937).

CASTLE, W. E. 1919. Piebald rats and selection, a correction. *Amer. Nat.*, 54· 370-376.

COCKAYNE, E. A. 1924. The distribution of fluorescent pigments in Lepidoptera. *Trans. Ent. Soc. Lond.*, 1924. 1-19.

——. 1932. A new explanation of the genetics of sex-limited inheritance in butterflies. *Entomology*, 65: 169–176.

COUTAGNE, G. 1895, 1896 Récherches sur le polymorphisme des mollusques de France. *Ann. Soc Agr Sér. Lyon*, 2· 397 460; 3 291-458

COTT, H. B. 1940. *Adaptive Coloration in Animals.* London: Methuen.

DACQUÉ, E. 1935. *Organische Morphologie und Palaeontologie* Berlin Gebr Bornträger.

DOBZHANSKY, T. 1941 *Genetics and the Origin of Species.* 2d ed. New York. Columbia Univ. Press.

EIMER, T. 1897. *Orthogenesis der Schmetterlinge.* Leipzig. Engelmann.

ELTRINGHAM, H 1910 *African Mimetic Butterflies.* Oxford: Oxford Univ. Press.

FEDERLEY, H. 1905. Lepidopterologische Temperaturexperimente. *Festschr. Palmén. Helsingfors,* 1–117.

——. 1920 Die Bedeutung der polymeren Faktoren für die Zeichnung der Lepidopteren. *Hereditas,* 1: 221–269.

FISHER, R. A. 1927. On some objections to mimicry theory. Statistical and genetic. *Trans. Ent. Soc. Lond.*, 75: 269–278

——. 1930a. The evolution of dominance in certain polymorphic species. *Amer. Nat.*, 64: 385–406.

——. 1930b. *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.

FORD, E. B. 1936. The genetics of *Papilio dardanus*

(Brown) Lep. *Trans. Roy Ent. Soc. Lond.*, 85: 435–466.

Ford, E. B. 1937. Problems of heredity in the Lepidoptera. *Biol. Rev.*, 12: 471–503.

——. 1940a. Genetic research in the Lepidoptera. *Ann. Eugen.*, 10: 227–252.

——. 1940b. Polymorphism, in Huxley's *The New Systematics*. Oxford. Clarendon Press.

Fryer, J. C. F. 1913. An investigation by pedigree breeding into the polymorphism of *Papilio polytes*. *Philos. Trans.* B, 204 227–254.

——. 1928. Polymorphism in the moth *Acalla camariana* Zeller. *J. Genet.*, 20: 157–178.

——. 1931. Further notes on the tortricid moth *Acalla camariana* Zeller. *J. Genet.*, 24. 195–202.

Gerould, T. H 1916. The inheritance of seasonal polymorphism in butterflies *Amer. Nat.*, 50: 310–316.

——. 1923. Inheritance of white wing color, a sex-limited (sex-controlled) variation in yellow pierid butterflies *Genetics*, 8: 495–551

Goldschmidt, R. 1912. Bemerkungen zur Vererbung des Geschlechtspolymorphismus *Z. ind. Abst Vererl.*, 3. 79–88

——. 1920a. *Die quantitative Grundlage von Vererbung und Artbildung.* Berlin Julius Springer.

——. 1920b *Mechanismus und Physiologie der Geschlechtsbestimmung.* Berlin· Gebr Bornträger.

——. 1920c. Untersuchungen zur Entwicklungsphysiologie des Flugelmusters der Schmetterlinge. *Arch Entwmech. Org.*, 47 1–24.

—— 1921 Erblichkeitsstudien an Schmetterlingen III. *Z ind Abst -Vererb.*, 25. 89–163

—— 1922 Untersuchungen uber Intersexualitat II *Z. ind Abst Vererb.*, 29 145 185

——. 1923. Einige Materialien zur Theorie der abgestimmten Reactionsgeschwindigkeiten. *Arch. mikr Anat*, 98 292 313.

—— 1924. Erblichkeitsstudein an Schmetterlingen IV. *Z ind. Abst -Vererb*, 34: 229 244.

——. 1927. *Physiologische Theorie der Vererbung.* Berlin: Julius Springer.

——. 1929a. *Die sexuellen Zwischenstufen.* Berlin· Julius Springer.

——. 1929b. *Einfuhrung in die Vererbungswissenschaft.* 5th ed Berlin· Julius Springer.

——. 1934. *Lymantria. Bibl. Genet.*, 11· 1–186.

——. 1935. Gen und Ausseneigenschaft I, II. *Z. ind. Abst.-Vererb.*, 69. 38–131

——. 1938a. *Physiological Genetics.* New York: McGraw Hill.

——. 1938b. A note concerning the adaptation of geographic races of *Lymantria dispar* L. to the seasonal cycle in Japan. *Amer. Nat*, 72· 385–386.

——. 1940. *The material basis of evolution.* New Haven: Yale Univ. Press.

——, and Fischer, E. 1922 *Argynnis paphia-valesina*, ein Fall geschlechtscontrollierter Vererbung. *Genetica*, 4: 247–278.

Haase, E. 1891–93. Untersuchungen über die Mimicry. *Bibl. Zool.*, 3: 1–120; 1–193.

Henke, K. 1933. Untersuchungen an *Philosamia cynthia* Drury zur Entwicklungs physiologie des Zeichnungsmusters auf dem Schmetterlingsflügel. *Arch. Entwmech. Org*, 128: 15–107.

——. 1933a. Zur vergleichenden Morphologie des centralen Symmetriesystems auf dem Schmetterlingsflügel. *Biol. Zbl.*, 53: 165–199.

——. 1933b Zur Morphologie und Entwicklungsphysiologie der Tierzeichnungen. *Naturwiss.*, 21: 633–690.

——. 1936 Versuch einer vergleichenden Morphologie des Flugelmusters der Saturniden auf entwicklungsphysiologischer Grundlage. *Nova. Acta Leop. (n. F.)*, 4. 1–137.

——. 1937. Untersuchungen zur Genetik und Entwicklungsphysiologie der Flügelform bei der Mehlmotte *Biol Zbl.*, 57 449–507.

——, Finck, E. von and Ma, S. Y. 1941. Über sensible Perioden fur die Auslosung von Hitzemodifikationen bei *Drosophila* und die Beziehungen zwischen Modificationen und Mutationen. *Z. ind. Abst -Vererb.*, 79. 267–316.

Huxley, J. S. 1940. *The New Systematics.* Oxford: Clarendon Press.

——. 1943. *Evolution. The Modern Synthesis.* London and New York: Harper and Brothers.

Jordan, K. 1911 The systematics of some Lepidoptera which resemble each other, and their bearing on general questions of evolution. *Mem. I. Int. Cong. Ent. Bruxelles*, 385–444.

Kaye, W. J 1906. Notes on the dominant Mullerian group of butterflies from the Potari District of British Guiana. *Trans. Ent. Soc. Lond.*, 1906: 411–440.

Kohler, W 1932. Die Entwicklung der Flügel bei der Mehlmotte *Ephestia kuhniella* Zeller mit besonderer Berucksichtigung des Zeichnungsmusters. *Z. Morph. Oekol.*, 24: 582–681.

Kosminsky, P. 1909. Einwirkung ausserer Einflusse auf Schmetterlinge. *Zool. Jb. (Syst.)*, 27 361–390.

Kühn, A. 1926. Über die Änderung des Zeichnungsmusters von Schmetterlingen durch Temperaturreize und das Grundschema der Nymphalidenzeichnung. *Nachr. Ges. Wiss Gottingen*, 1926: 120–141.

——, and Engelhardt, M von. 1936. Über die Determination des Flugelmusters bei *Abraxas grossulariata* L. *Nach. Ges Wiss. Gottingen*, (n F. Z.). 171–199.

——, and Henke, K. 1929–1936 Genetische und entwicklungsphysiologische Untersuchungen an der Mehlmotte *Ephestia kuhniella* L. *Abh. Ges. Wiss Gottingen. Math. Phys. Kl.* (n. F.), 15: 1–121; 125–219; 225–272

Lang, A. C. 1904. Über Vorversuche zu Untersuchungen über die Varietätenbildung von *Helix* *hortensis* Müller und *Helix nemoralis* L. *Festschr. Ernst Häckel,* 439–506.

Lang, A. C. 1906. Über die Mendelschen Gesetze, Art und Varietätenbildung, Mutation und Variation insbesondere bei unseren Hain und Gartenschnecken. *Verh. Schweiz. Naturf. Gesellsch. Luzern.*

——. 1908. Über die Bastarde von *Helix hortensis* Müller und *Helix nemoralis* L. *Festschr. Univ. Jena.*

——. 1911. Fortgesetzte Vererbungsstudien. *Z. ind. Abst.-Vererb.,* 5: 97–111.

Lus, T. 1926. On the inheritance of color and pattern in lady beetles *Adalia bipunctata* L. and *Adalia decempunctata* L. *Biol. Zh.,* 1: 153–164.

Mayr, E. 1942. *Systematics and the origin of species.* New York: Columbia Univ. Press.

de Meijere, T. C. H 1910. Über Jacobson's Züchtungsversuche betreffend den Polymorphismus von *Papilio memnon* L. *Z. ind. Abst.-Vererb.,* 3: 161–181.

Nicholson, A. J. 1927. A new theory of mimicry in insects. *Austral. Zool.,* 5: 10–104.

Poulton, E. B. 1906. Mimetic forms of *Papilio dardanus* (*merope*) and *Acraea jonstoni. Trans. Ent. Soc. Lond.,* 1906: 281–322.

——. 1927. On certain effects of shock upon insect development. *Proc. Ent. Soc. Lond.,* 2: 79–90.

Punnett, R. C. 1915. *Mimicry in Butterflies.* Cambridge: Cambridge Univ. Press.

Robson, G C. 1928. *The Species Problem.* London: Oliver and Boyd.

——, and Richards, O. W. 1936. *The Variation of Animals in Nature.* London: Longmans, Green and Co.

Schwanwitsch, B. N. 1924. On the ground plan of wing pattern in Nymphalids and certain other families of the Rhapalocerous Lepidoptera. *Proc. Zool. Soc. Lond.,* 1924: 509–528.

——. 1926. On the modes of evolution of the wing pattern in Nymphalids and certain other families of the Rhopalocerous Lepidoptera. *Proc. Zool. Soc. Lond.,* 1926: 493–508.

——. 1928. Studies upon the wing pattern of *Pierella* and related genera of South American Satyridan butterflies. *Z. Morph. Oekol. Tiere,* 10: 433–532.

——. 1929. Evolution of the wing pattern in palearctic Satyridae I. *Z. Morph. Oekol. Tiere,* 13: 559–654.

——. 1929a. Two schemes of the wing pattern of butterflies. *Z. Morph. Oekol. Tiere.,* 14: 36–58.

——. 1931. Evolution of the wing pattern in palearctic Satyridae II. *Z. Morph. Oekol. Tiere,* 21. 316–408.

——. 1935. Evolution of the wing pattern in palearctic Satyridae III. *Acta Zool.,* 16: 143–281.

——. 1936. Symmetry in the wing pattern of some Papilionid butterflies. *The Entom.,* 64: 7–12.

Seitz, A. 1907ff. *The Macrolepidoptera of the World.* Stuttgart. Enke.

Shull, F. A. 1936. *Evolution.* New York: McGraw-Hill.

——. 1937. The needs of the mimicry theory. *Science* 85: 496–498.

Standfuss, M. 1896. *Handbuch der palaearktischen Grossschmetterlinge.* Jena: Fischer.

——. 1909. Hybridisations experimente. *Et. Lepidoptérol. comp. de Charles Oberthuer.*

——. 1910. Die alternative oder discontinuierliche Vererbung und ihre Veranschaulichung an den Ergebnissen von Zuchtexperimenten mit *Aglia tau* und deren Mutationen. *Dtsch. Ent. Natbibl.* 1.

Süffert, F 1927. Zur vergleichenden Analyse der Schmetterlingszeichnung. *Biol. Zbl*, 27: 385–413.

——. 1929a. Die Ausbildung des imaginalen Flügelschnittes in der Schmetterlingspuppe. *Z. Morph. Oekol. Tiere,* 14: 338–359.

——. 1929b. Morphologische Erscheinungsgruppen in der Flügelzeichnung der Schmetterlinge insbesondere die Querbindenzeichnung. *Arch. Entwmech. Org.* 120: 299–383.

Vavilov, N. 1922. The law of homologous series in variation *J. Genet.,* 12. 47–69.

Watkins, A. E. 1935. *Heredity and Evolution.* London: John Murray.

THE EVOLUTION OF MALE HAPLOIDY

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INTRODUCTION

THE usual mode of sexual reproduction in Metazoa is that in which both sexes are produced from fertilized eggs. In certain groups of invertebrate animals, however, there occurs a type of reproduction in which the males are normally *impaternate* (fatherless), being developed from unfertilized eggs. These eggs have undergone reduction in chromosone number as if in preparation for fertilization, but since fertilization is lacking, the males developing from them have the reduced or haploid set of hereditary factors. The eggs will, if fertilized, normally develop into females. Hence the females are biparental in inheritance, the males uniparental. The Silesian bee breeder Johannes Dzierzon set forth this principle in 1845 with respect to the honey-bee, stating that drones, the males, come from unfertilized eggs, while workers and queens, the females, come from fertilized eggs.

The production of animals from fertilized eggs has been called *zygogenesis* in distinction to *parthenogenesis*, which refers to the development of an egg without fertilization. There are other types of parthenogenesis besides that described by Dzierzon. Unfertilized eggs may start as haploids and subsequently acquire the diploid number of chromosomes in some stage of cleavage, or they may start as diploids. The end result, in either case, is a fatherless (*impaternate*) but diploid animal. The evolution ot such animals, interesting as it is, does not present the difficulties involved in explaining how the regular production of haploid adults has come about. In the case of impaternate diploids the chief problem is one of origin. In the case of impaternate haploids there are added, among other problems, those of survival with reduced chromosome number, of sex determination, and of spermatogenesis in the haploid male. Aside from the haploid males regularly produced in six or seven groups of invertebrates, there have been, with one or two exceptions, no known haploid adult animals. In contrast, diploid and polyploid impaternates are known to occur with more or less frequency and as independent events in many, if not most, of the larger groups of Metazoa. The origin of these will be discussed because of its possible bearing on the origin of male haploidy. Their method of sex determination is entirely orthodox, while that of haploid males involves a genetic mechanism essentially different.

Many of the hazards involved in the origin and survival of male haploidy which must have been overcome by evolution were stated by Schrader and Hughes-Schrader in 1931, in a discussion of the subject based on data available at that time. During the last decade, considerably more data have been accumulated, especially bearing upon sex determination in haploid animals, the problem which has been most difficult to explain, and it is for this reason that a review of the matter is now timely.

Different groups and species of animals combine different types of parthenogenesis with bisexual reproduction in their life cycles in various complicated ways. An excellent review of the subject has been given by Vandel (1931a), and no attempt will be made here to summarize what he has presented or to review more recent literature in detail. References given in this paper are selected, for the most part, from recent publications which show the extent and diversity of parthenogenesis, and thus have a bearing directly or indirectly upon the evolution of male haploidy, or in other words, the evolution of reproduction according to Dzierzon's Law.

Definitions

A considerable terminology has been developed in connection with the subject of parthenogenesis in which ambiguities are present, unfortunate, but certainly unavoidable in a science developed in many lands and published in many languages. In order to orient the reader and to assist in expressing ideas more briefly, some definitions are given of terms to be used repeatedly.

The author follows Ray Lankester in using the term *impaternate* rather than parthenogenetic for the fatherless offspring developed from the unfertilized egg. Parthenogenesis may be *natural* (*spontaneous*) or it may be *artificial* (induced by some artificial stimulus). It may be *incomplete* (rudimentary), the embryo dying before maturity, or it may be complete, involving viability to the adult stage. It may be *obligatory*, occurring from a type of egg that cannot normally be fertilized, or it may be *facultative*, if the egg may develop whether fertilized or not. With reference to the sex of the impaternate offspring, parthenogenesis includes *arrhenotoky*, production of impaternate males, *thelytoky*, production of impaternate females, and *deuterotoky*, production of both sexes parthenogenetically.

The term *tychoparthenogenesis* (the prefix is derived from the Greek τύχη meaning chance, luck, or the favor of the gods) has been used for irregular cases occurring occasionally in zygogenetic species, either in nature or in experimental breeding (*Lymantria dispar* of Goldschmidt, 1917). The word may be extended to include a condition which may be regularly induced merely by preventing the female from mating (Tettigidae of Nabours, 1929, 1930) and which thus indicates a natural genetic tendency toward parthenogenesis. While the latter is, in a sense, induced tychoparthenogenesis, it is, of course, natural and facultative (spontaneous under the circumstances) rather than artificial (induced by artificial stimulus). With respect to sex of offspring, tychoparthenogenesis includes *tychothelytoky* and *tychodeuterotoky*. *Tychoarrhenotoky* has not been demonstrated. The possibility of its occurrence and the significance of the other two will be discussed in connection with sex determination.

Parthenogenesis may be *constant*, occurring in each successive generation, or it may be *cyclic*, in which case one or more parthenogenetic generations alternates with a bisexual. In cyclic parthenogenesis (*heterogony*) the parthenogenetic or agamic generation, the generation reproducing parthenogenetically, consists entirely or almost entirely, of females. The individuals of the bisexual generation, both males and (*gamic*) females, are impaternate. Parthenogenesis may occur as a *general* condition throughout the range of the species, or it may be *geographic*, in which case the parthenogenetic race occupies a different area from the bisexual. Males may be absent or very rare (*spanandry*) within the range of the parthenogenetic race.

With reference to meiotic phenomena in the egg, parthenogenesis may be *haploid* or *diploid*. In diploid parthenogenesis meiosis may be omitted altogether, there may be but a single oocyte division or, if both divisions occur, there may be fusion of two of the resulting haploid nuclei (*parthenogamy*). Diploid parthenogenesis may also be brought about by doubling of chromosome number in oogonial mitosis (*endomitosis*) to form the tetraploid number. Subsequent synapsis and two oocyte divisions give rise to a diploid egg which undergoes cleavage. The result, in any case, is a diploid individual which has been diploid from its beginning. Diploid parthenogensis may be said to result in a *zygote*, which in some cases is heterozygous, in others homozygous for genes that were heterozygous in the mother.

In triploid and polyploid parthenogentic races or species oogenesis takes place according to various methods as in diploid parthenogenesis.

In haploid parthenogenesis, meiotic phenomena in the egg are normal, with two oocyte divisions resulting in a haploid nucleus. The offspring is not, however, necessarily haploid, although starting as such, since chromosome doubling by endomitosis or by fusion of nuclei may occur during cleavage. Higher multiples of the haploid set are reported for some tissues than for others. Whatever the ultimate cytological conditions may be, the individual may be designated an *azygote* and, barring mutation, will breed true, all sperms or eggs produced by it being of identical genetic composition, since it originates from a haploid cell.

The term diploid parthenogenesis has often been used to include all cases in which the impaternate offspring have been judged on purely morphological grounds to be diploid, even though this diploidy results from "regulation" after meiotic reduction. This usage, developed before application of the genetic point of view, has caused much confusion and useless discussion, since chromosome number sometimes fluctuates in different tissues, and the criteria for haploidy are frequently very uncertain. In azygotes resulting from tychoparthenogenesis or from artificial parthenogenesis, this fluctuation is often very great. I believe that the extension of the term haploid parthenogenesis to include all cases of origin from a single reduced maternal nucleus in animals should be helpful, by emphasizing a distinction of fundamental genetic significance between azygotes, whether haploid or not, and impaternate zygotes, which are diploid (or polyploid) in origin.

I have used the terms haploid or diploid as applied to azygotes just as I have used the terms diploid or polyploid for zygotes. These terms must be understood to be relative. Actually we do not know that any "diploid" animal is diploid in all of its tissues, and we do know that polyploid cells and tissues occur in many diploids. Similarly, we cannot say that any "haploid" animal resulting from haploid parthenogenesis is haploid throughout. The azygotes resulting from tychoparthenogenesis are, at least for the most part, diploid and possess the type of gametogenesis characteristic of normal diploid zygotes. The azygotes, males, produced by haploid arrhenotoky in the regularly established parthenogensis of Dzierzon's Law and the subject of discussion of this paper, are only more-or-less haploid, the drone bee being less, in fact apparently diploid with some polyploid tissues. Whatever the chromosome count may be in "male haploidy," meiosis is peculiarly modified or eliminated in the males so that spermatogenesis is of the haploid type.

While tychoparthenogenesis and the parthenogenesis involved in male haploidy are both facultative, they differ in that the former is poorly adapted, with many inviable cases of rudimentary parthenogenesis, while the latter is highly perfected, reproductively economical, facultative in the highest degree.

The parthenogenesis of male haploidy is to be contrasted with obligate arrhenotoky occurring in the male-producing females of the parthenogenetic generation preceding the bisexual in some of the groups with cyclic parthenogenesis. Other parthenogenetic females of these groups may be obligately thelytokous or deuterotokous.

In groups with constant parthenogenesis facultative arrhenotoky may be combined with deuterotoky. Fertilized eggs will then produce females, unfertilized will produce either males or females.

Many of the terms defined above are applied in various ways to individuals, fraternities, generations, races, species, or groups of higher taxonomic order, and this diversity of usage by different authors makes it difficult to clarify the subject. An individual of either sex may be either biparental or impaternate. A fraternity, generation, race, species, etc., may be either bisexual, consisting of males and females, or unisexual, made up of a single sex. The occurrence of induced parthenogenesis or of facultative parthenogenesis in a female, a race, a species, or a generation does not make it "parthenogenetic," for this term is used *sensu stricto* to indicate that the female or group is obligately parthenogenetic, that *all* offspring are impaternate. Thus a frog whose eggs are pricked and thereby stimulated to develop parthenogenetically does not become, through this process, different from any other frog, and is not said to be parthenogenetic. In the literature on artificial parthenogenesis the impaternate offspring are frequently designated as parthenogenetic, but this ambiguous usage is here avoided in accordance with the suggestion of Ray Lankester mentioned above.

A male should not be described as parthenogenetic, arrhenotokous, deuterotokous, thelytokous, or zygogenetic, but may belong to a race, a species, or a heterogonic generation characterized by any one of these terms. Exceptional or spanandric males occur in parthenogenetic (thelytokous) groups, but, except for these males, a parthenogenetic generation, race, or species consists of females only. Races or entire species are either parthenogenetic (female), arrhenotokous, deuterotokous, or zygogenetic. Parthenogenetic groups of taxonomic order higher than species do not occur, but such groups may be arrhenotokous, deuterotokous, or zygogenetic. A group (generation, race, species, etc.) reproducing according to Dzierzon's Law is said to be arrhenotokous. Thus the honey-bee *Apis mellifica* s an arrhenotokous, not a parthenogenetic or a zygogenetic, species. There are, however, races of the honey-bee that may produce females as well as males from unfertilized eggs. Such races are deuterotokous. The females of many species of grasshoppers are described as facultatively thelytokous because they produce females if they are unmated. The females of several species of moths are facultatively deuterotokous, producing impaternate offspring of both sexes. A certain parasitic wasp, *Nemeritis canescens*, although belonging to the arrhenotokous insect order Hymenoptera, is obligately thelytokous, a parthenogenetic species with males unknown. The European race of a certain stick insect, *Carausius morosus*, although belonging to the zygogenetic insect order Orthoptera, is obligately thelytokous, a parthenogenetic race with rare, spanandric, males. The ancestral Asiatic type of the same species is bisexual and zygogenetic. This species therefore exhibits geographic parthenogenesis.

Use of the expressions arrhenotokous, deuterotokous, or thelytokous parthenogenesis is grammatically incorrect, redundant, because these adjectives imply parthenogenesis.

Extent of Occurrence of Male Haploidy

Production of males by haploid arrhenotoky is a stable mode of bisexual reproduction functioning quite as successfully as the more frequent method of zygogenesis of both sexes. It occurs in rotifers (Miller, 1931; Shull, 1929; Tauson, 1927; Wesenberg-Lund, 1923, 1930; Whitney, 1929), certain groups of mites (André, 1935; Cooper, 1937, 1939; Pätau, 1934, 1936; Putnam, 1939; Schrader, 1923), thrips (Davidson and Bald, 1931; Shull, 1917), white-flies (Morrill and Back, 1911; Schrader, 1920, 1926; Stoll and Shull, 1919; Thomsen, 1927), a certain tribe of scale-insects (Hughes-Schrader, 1927, 1930; Schrader and Hughes-Schrader, 1926), the beetle *Micromalthus* (Scott, 1936, 1938, 1941) and insects of the order Hymenoptera.

Most insects of this last-named order are much larger and more conspicuous than insects in the other orders and have, accordingly, received more attention from entomologists, cytologist, and students of heredity. For this reason, the Hymenoptera have contributed more than any other group to our understanding of the problems connected with male haploidy. Since reference will be made frequently to various members of the different subgroups of this order, they will now be very briefly characterized.

The order Hymenoptera is popularly said to include wasps, ants, and bees, but these divisions are by no means correlative. The great majority of species and major divisions are often called wasps. It is also often supposed that the order is characteristically made up of social insects. This is a misconception. Of the two large suborders, the Chalastogastra includes the more primitive species, plant feeders with caterpillar-like larvae, the horn-tails and saw-flies. Under the suborder Clistogastra, with maggot-like larvae, there are seven superfamilies. Four of these, Ichneumonoidea, Proctotrupoidea, Chalcidoidea and Evanioidea, include the vast majority of described species of the order, wasps which are largely parasitic on other insects and hence of great value economically. The gall-forming wasps and their relatives, Cynipoidea, make up the fifth superfamily. The members of the two remaining superfamilies, the aculeates or stinging Hymenoptera, are for the most part, wasps and solitary, as are all those previously mentioned. Of the fourteen families of the aculeate Vespoidea, only two show social development, the Formicidae or ants, which are all social, and the Vespidae or hornets, yellow jackets, etc., with some species solitary, some social in varying degrees, and with social organization polyphyletic within the group.

The seventh superfamily of the Clistogastra the aculeate Sphecoidea, includes three families of digger wasps, all solitary, and five families of bees, largely solitary but showing polyphyletic evolution of social life.

The entire order, irrespective of social organization, from lowest to highest in all of its divisions is characterized by parthenogenesis mixed with sexual reproduction (Peacock and Gresson, 1931; Sanderson, 1932; S. G. Smith, 1941). Biparental males (diploid) have not been reported from nature in any species, and meiotic phenomena in the male, as well as spermatogonial and somatic mitoses, indicate male haploidy. Dzierzon's Law applies as the rule. The sterile biparental males regularly occurring in the parasitic wasp *Habrobracon*, under conditions of inbreeding and "domestication" which will be discussed later, are not considered here. Oogenesis in all male-producing eggs is regular, with two oocyte divisions giving rise to the haploid nucleus. Naturally occurring exceptions to Dzierzon's Law are all in the direction of thelytoky, and in this case the oocyte divisions are variously modified. Even in the honey-bee, the species studied by Dzierzon and on which he based his principle, thelytokous races occur in which workers (females) produce workers without mating.

Many species in diverse groups are entirely thelytokous, females producing females indefinitely by diploid parthenogenesis with males entirely unknown (B. R. Speicher, 1937). In other species thelytoky is geographic, the female race occupying a newer region than the bisexual (arrhenotokous) (Brues, 1928; S. G. Smith, 1941). This condition is supposed to aid in the rapid spread of the species. Bisexual reproduction may be resumed later in the new territory.

In several gall-making wasps among the

Cynipoidea, alternation of a bisexual with an agamic female generation takes place (heterogony). The sexual females may be very different in appearance from the agamic, so that some have been described under generic names different from their own offspring. In the more highly evolved species of this group, a single agamic female produces either males or females but not both, and Doncaster (1916) has shown that from a single mating of a sexual female there are obtained only male-producers or only female-producers Among the less specialized species a single agamic female may produce both males and females, and the tendency to produce one sex only appears to have evolved gradually within the group (Patterson, 1928a). In the agamic female generation parthenogenesis is obligatory, and the females, if introduced to males, refuse to mate. A few functionless males with weak mating instincts occur in this generation, probably from unfertilized eggs of the sexual females. They have been shown to be haploid, as are the normal males of the sexual generation (Patterson, 1928b).

In many species, among the minute egg parasites Chalcidoidea and Proctotrupoidea, polyembryony takes place, a single egg giving rise to more than one embryo, with numbers ranging from a few to many hundreds. Dzierzon's Law applies here, so that males only are produced if the egg is unfertilized, while a fertilized egg gives rise to a female brood. However, it has been shown that a few males, haploid, may sometimes appear in a female brood, indicating probable somatic reduction of chromosome number in the germ mass (Patterson and Hamlett, 1925)

Since parthenogenesis and male haploidy characterize the entire order from the relatively primitive horn tails and saw-flies to the highly specialized parasites and the social wasps, ants, and bees, it must have appeared very early in evolution.

Taxonomically, the Hymenoptera are singularly isolated, with highly specialized wing venation even in the most primitive members, which show no relationship with any other orders. In the paleontological record there is also no evidence of relationship to other groups. The earliest forms occur in the Upper Jurassic strata and include both the plant-feeding Chalastogastra and primitive members of the parasitic groups in the Clistogastra,—Ichneumonoidea, Proctotrupoidea, and Evanioidea. Since several groups under both suborders are found in the Jurassic and since all known living Hymenoptera reproduce parthenogenetically, these extinct species must also have done so, unless we are to assume that parthenogenesis originated independently several times and spread through the entire order, which is highly improbable.

Fossil Hymenoptera are lacking in the Cretaceous period. The earliest aculeates date from the Eocene, at which time all the parasitic groups are also abundant. Among the ants, sexual females were distinct from the workers in the Tertiary, but polymorphism was absent among the latter, and differences separating the true workers from the soldiers were not evident until the Pleistocene.

PROBLEMS INVOLVED

Before an hypothesis is suggested to explain the steps in development of male haploidy, it will be necessary to consider certain problems concerning parthenogenesis, and some of the known facts which may throw light upon them. These problems may be discussed under five headings, as follows: (1) induction of parthenogenetic development in eggs; (2) viability of the azygote; (3) meiosis in the haploid male, (4) sex determination; (5) haploidy of the azygous male. The first two of these may be regarded as initial steps in the attainment of male haploidy. The remaining three problems will be considered before additional steps are presented.

Induction of Parthenogenetic Development in Eggs

Plants, with their normal alternation of an azygotic (gametophytic) with a zygotic (sporophytic) generation, have no block to post-meiotic mitosis. In animals this block is regularly established, with insurance thus added to syngamy but frequent lapses occur, initiating parthenogenesis. There is no need to discuss the causes of these lapses, which are the subject of innumerable experiments by physiologists and which fill volumes of research publications. Effective factors are chemical constituents of the water, temperature changes, and mechanical stimuli such as shaking or pricking the eggs, in addition to hereditary constitution. Lack of the block or its breakdown, as exemplified by the spore of a fern or the egg of a bee, is no greater problem than establishment of the block, as it occurs in the egg of a fly, for example.

In addition to experiments on artificial parthenogenesis, the wide scattering of tychoparthenogenesis in different groups indicates the frequency of independent occurrence of this breakdown. Moreover, the presence of tychoparthenogenesis in some groups and in certain species, contrasted with its absence from others, demonstrates a racial or genetic basis.

Viability of the Azygotes

In presenting definitions concerning parthenogenesis, the distinction was made between haploid and diploid parthenogenesis, and it was pointed out that the former leads, not necessarily to a haploid animal, but often to a diploid azygote. In fact, tychoparthenogenesis is haploid, at least in the majority of cases, but in all cases the end result is a diploid. Most diploid zygous animals appear to carry recessive lethal genes which tend to be retained in the species because of their recessiveness. With the occasional development, in a normally zygogenetic species, of an unfertilized haploid egg such lethal genes disclose their presence, even though the egg develops into a diploid (homozygous) azygote. A high mortality of these azygotes (incomplete parthenogenesis) takes place, so that selection against recessive lethal genes must be very severe in tychoparthenogenesis. Many cases of incomplete parthenogenesis may be expected to occur in a zygogenetic species before an adult azygote appears. Having appeared, it is free from recessive lethals and ready to carry on should other conditions be conducive to that end.

The occurrence of such an azygote in the first place, together with its survival to maturity, indicates that it has certain genes required for successful parthenogenetic development. If it can reproduce, its offspring should, on the average, carry more genes tending toward parthenogenesis than the average of sexually produced individuals. Hence we might expect parthenogenetic races to appear by natural selection among the descendents of sporadically occurring diploid azygotes arising from haploid parthenogenesis, as well as of impaternates produced by diploid parthenogenesis in which recessive lethals would have no effect.

One definite condition which must be fulfilled (and which is undoubtedly accomplished by natural selection) if azygotes are to be viable, is a satisfactory surface-volume relationship in cells. Viable haploid sporophytes have been obtained in many species of plants without difficulty, whereas in normally diploid animals survival of a haploid is very infrequent. Fankhauser (1938) has been able by cold treatment to initiate haploid parthenogenesis in salamanders, but only one survived to a stage beyond sex differentiation. Surface-volume relationships in animal cells may be such that they place a much greater hazard on deviations from normal chromatin quantity than occurs in plants.

One method of regulation of the surface-volume relationship is by a doubling of chromosome number in the cleavage of an egg originally haploid, resulting in a restored but azygous diploid. Artificial parthenogenesis in frogs illustrates the problem of attainment of viability by chromosome doubling after parthenogenesis. Development is initiated by pricking the eggs (Kawamura, 1939; Parmenter, 1940). A small proportion of these gives off two polar bodies and undergoes cleavage. Embryos are highly inviable, but some have formed tadpoles, and a very few have metamorphosed. Of those not completing development, some are haploids, some diploids, and others are haplo-diploid or diplo-triploid mosaics, and even tetraploid tissue has been found. The increases in chromosome number come about before the first cleavage, during cleavage, or in later embryonic stages.

Because a large proportion of the impaternate tadpoles have been haploid and because others have had tissue in part haploid, it is certain that a majority, and perhaps all, were azygotes. The possibility is not excluded, however, that meiotic regulatory processes or parthenogamy from a polar body may have occurred in some, retaining maternal heterozygosis, and bringing about diploid parthenogenesis. It has not in all cases been noted that two polar bodies were extruded.

The cytological conditions of tychoparthenogenesis as it occurs in many invertebrates appear to be very similar to those in experimental parthenogenesis of frogs. There is a high mortality of developing embryos, and the survivors are diploid.

Before the remaining problems involved in attainment of male haploidy are discussed, certain types of diploidy in male Hymenoptera may be considered. This matter is taken up here because of its bearing on the viability of azygotes.

Chromosome number in the honey-bee has been a moot question for many decades. Nachtsheim (1913) summarized and discussed the various views and was able to dispose of many of the cruder and less adequately supported hypotheses. His cytological study appears to be of the highest order. He regards sixteen as the haploid number of chromosomes and thirty-two as the diploid. Because there is reduction to eight in the primary oocyte, I prefer to regard eight as the haploid, and sixteen as the diploid chromosome number, and I consider his higher numbers as due to regulative splitting. Nachtsheim calls the first oocyte division reductional. By this he may mean either that the number of chromosomes is halved or that paternal elements are segregated from maternal. Presumably genes may segregate in either division, as in other forms.

In the following account I am disregarding Nachstsheim's terminology and his diagrams and am basing my statements on his excellent drawings of the actual material. Oogenesis is regular. There are sixteen chromosomes in the oogonia. Oocyte I metaphase is not shown. Eight dyads go to each pole in oocyte I anaphase. These dyads appear in both metaphase II spindles and divide into monads, eight of which pass to each pole in anaphase II.

Cleavage of the unfertilized male-producing egg shows that most of the chromosomes have already split in a regulative process, so that the number becomes sixteen, and this number is also seen in the blastoderm. It may be further increased in later stages. The chromosomes tend to lie in sister pairs because of their origin through regulative splitting.

Spermatogonia are not shown. There are sixteen dyads in the nucleus of the abortive spermatocyte I division. The spermatocyte II nucleus is divided equally, eight dyads going to each pole in anaphase. The chromatids may be separated so that they already appear as eight pairs of monads.

Cleavage in the fertilized egg shows thirty-two chromosomes, and approximately this number may be seen in the blastoderm. There is much discussion about the somatic chromosome numbers, some authors finding up to sixty-four (octoploid) in certain tissues of both sexes. It may well be that, due to regulation, the drone bee has, in general, the same chromosome numbers as the female, although it originates from a haploid egg. Nuclei of the male approximate in size those of the female (Oehninger, 1913; Nachtsheim, 1913). The fact that all the chromosomes are duplicated keeps the genic balance similar in all male tissues.

The number sixteen in spermatocyte I and in cleavage of the unfertilized egg is undoubtedly regulative. Reduction to eight in spermatocyte II is perhaps the last echo of ancestral male haploidy. This type of polyploidy, seen also in many tissues of other animals, may be called somatic polyploidy. It has no bearing on genetic ratios, so that the male bee should breed as a haploid, the female as a diploid. The number of linkage groups should be eight.

A second method of regulation for surface-volume relationships might be by increase in chromosome size. Size of nuclei and size of cells might thus be increased in the haploid male to approximate conditions in the female. Somatic haploidy has been demonstrated for certain tissues in certain species, but it is possible that regulation by doubling may take place in other tissues. Cleavage and gonial nuclei of males have been shown to have half as many chromosomes as those of females in several forms. This proves to be the case in the Ichneumonoid wasp *Habrobracon* in which wing cell size of "haploid" males approximates that of females (B. R. Speicher, 1935). The chromosome number in wing cells is, however, not known.

At present, many workers in this field of study take for granted haploidy of the males produced according to Dzierzon's Law, but considerable doubt has been expressed at various times in the past as to whether haploid organisms could be viable. In view of the fact that gametophytes of plants are normally haploid, this doubt was restricted to viability of haploid forms of organisms that are normally diploid. Subsequently, after the demonstration of occasional haploidy in sporophytes of plants, the doubt was still expressed as to whether animals might survive as haploids. Cytological studies indicating somatic polyploidy of the drone honey-bee seemed to strengthen skepticism as to the viability of haploid Metazoa.

In order to "explain" the viability of males in the Hymenoptera despite their presumed or apparent haploidy, and also in order to account for certain cytological phenomena, the suggestion has been advanced that the "haploid" set of the males is fundamentally diploid. Since females have been shown to possess twice the male chromosome number, in certain tissues at least, it follows that females would be tetraploid.

In several of the lower Hymenoptera there is pairing, to some extent, among the chromosomes of the haploid set in the male. Sanderson (1932) calls attention to this in the saw-fly *Pteronidea ribesii,* in which the eight haploid chromosomes appear as three pairs and two odd chromosomes, and Dodds (1938) shows secondary pairing of the ten metaphase chromosomes in spermatocyte II in the gall-wasp *Neuroterus baccarum,* in which the female may have five groups of four "homologues" each. Greenshields (1936a) discusses this situation, arguing that in the Hymenoptera there may be a tetraploid female-diploid male relationship instead of a diploid-haploid. No such pairing is evident in chromosomes of the Ichneumonoid *Habrobracon,* and Speicher (1936) points out that genetic data show *Habrobracon* to breed as a haploid. Greenshields (1936b) says that there is conflict in the use of terms by cytologists and geneticists, and that the genetic "facts are by no means fatal to a theory of derived tetraploidydiploidy based on cytological findings." He regards the phenomena of pairing as vestiges in the evolutionary sense.

In the evolution of cytogenetic systems, duplication plays an important rôle. The entire complex of chromosomes of a normal diploid form may be doubled, resulting in an *autotetraploid.* These show irregular types of pairing, multiple synaptic complexes, etc. Sterile species hybrids may double their chromosome number, resulting in fertile *allotetraploids.* These tend to have more regular meiotic phenomena than autotetraploids and are, consequently, more fertile. Duplication of single chromosomes or of parts of chromosomes may occur, thus increasing the number or size of these structures. Genetic duplication is often evidenced by irregular types of segregation, but this condition may later be masked by selective elimination of certain types, by further chromosomal rearrangement, and by genic mutation, so that "normal" conditions reappear.

Genetic polyploidy, or more generally, genetic duplication, must be regarded as relative. It is impossible to determine how much duplication or how much deletion may have occurred in the past history of the chromosome set normal to any species. In polyploid series in several groups of plants, the gametic number of chromosomes has been called haploid. This haploid number may be various multiples of a more fundamental *monoploid* number which, presumably, acted as the haploid number of some ancestral type. The term haploid is, therefore, a relative term. It is not improbable that there may be remnants of genetic polyploidy in the lower Hymenoptera or in certain higher groups, but this has disappeared or does not exist at all in others. In any case, the somatic regulative polyploidy of the bee appears to be a very different phenomenon.

Meiosis in the Haploid Male

In addition to cleavage of the unfertilized egg and survival of the azygote to maturity, the species with haploid arrhenotoky have attained some sort of regulation or omission of meiosis in spermatogenesis, so that the sperm cells have the full haploid set. Irregular distribution of chromosomes, such as occurs in haploid sporophytes (Bleier, 1933), has been avoided. This may involve a certain amount of telescoping of premeiotic processes with postmeiotic. If meiosis be deleted altogether, what appears to be a spermatogonial cell must enter directly upon spermiogenesis. The condition is here analogous to that obtaining in the formation of antherozoids in moss or fern gametophytes, in which there is, of course, no heritage of meiosis.

Among the mites this condition is approximated. Schrader (1923) indicates no distinction in *Tetranychus bimaculatus* between spermatogonia and spermatids, each with three chromosomes, the haploid number. There is no growth stage, and meiosis is omitted. Pätau (1934, 1936), showing that the male of *Pediculoides ventricosus* is haploid with three chromosomes, did not follow spermatogenesis because he considered the cells too small. Presumably there is also no appreciable growth stage in the haploid "spermatocytes" of this mite.

In the homopteran insects of the family Aleurodidae or white-flies, the males are haploid. Schrader (1920) states that in the males of *Trialeurodes vaporariorum,* with eleven chromosomes, the "reduction" division is omitted, and the "equation" division is not differentiated from the last spermatogonial. Thomsen (1927), however, states that in *Aleurodes proletella* the spermatocytes have a clear growth stage, but there is only one meiotic division.

Most haploid males make some compromise with meiosis. This is effected in various ways in different groups.

In the one beetle shown to have haploid arrhenotoky, *Micromalthus debilis,* Scott (1936) studied spermatogenesis. The ten chromosomes of the abortive first spermatocyte anaphase move away from the single pole, with the attachment fibres lengthening. The second division is normal giving rise to two normal spermatids.

In the rotifer, *Asplanchna amphora*, Whitney (1929) showed thirteen chromosomes dividing in the first spermatocyte. Two types of sperms were found. The larger motile functional type, with thirteen chromosomes, the haploid number, develops directly from the secondary spermatocytes. A few of the secondary spermatocytes, however, divide with irregular distribution of chromosomes, to form spermatids with a small amount of chromatin. These develop into small non-functional spermatozoa. Tauson (1927) found but a single spermatocyte division with the reduced number twelve in *Asplanchna intermedia*, the second division being lacking. In this species she failed to find any rudimentary spermatozoa.

In the scale insects, Coccidae, of the tribe Iceryini, the males are haploid with two chromosomes. There is a single meiotic division of the first spermatocyte nucleus. The cytoplasmic division is suppressed and binucleate spermatids are thus produced from each of which two sperms develop (Hughes-Schrader, 1930). In the cottony cushion scale, *Icerya purchasi*, the females are secondarily modified into hermaphrodites. These have four chromosomes (Hughes-Schrader, 1927). The males, which are infrequent, are similar in spermatogenesis to males of the related species having females. Spermatogenesis of the haploid cells in the hermaphrodite gonad tallies in every respect with that in the males. Diploid cells in the hermaphrodite have also shown spermatogenesis in limited regions. It is clear that two divisions occur and that each sperm receives the haploid number. In several cysts of large cells there were four chromatin threads in various phases of condensation. Early telophases were found with four rods at each pole, and a few binucleate cells with four chromosomes in each nucleus. In the second anaphase two chromosomes go to each pole. As in the haploid spermatocytes of the hermaphrodites and of the males, there is no cytoplasmic division. The secondary spermatocytes from the diploid cells are therefore binucleate, with four chromosomes in each nucleus, and the spermatids are quadrinucleate, with two chromosomes in each nucleus. Each spermatid from the haploid spermatocytes develops two sperms and each spermatid from the diploid spermatocytes develops four sperms. In this form, apparently, normal meiosis with reduction can take place in spermatogenesis in diploid tissue.

With the exception of *Telenomus*, in which it is the second spermatocyte division that is abortive (Dreyfus and Breuer, 1944) the reported cases in the Hymenoptera show failure of nuclear division in the first spermatocyte, which usually gives off a small cytoplasmic bud. The second division is equal, and two sperm cells result, except that in the bees there is but one sperm cell which develops from the larger of the two very unequal spermatids. In the different hymenopterous species studied, details differ, as in degree of condensation of chromosomes during the first "division," in which also the cytoplasmic bud may be lacking.

That certain types of meiotic regulation become fixed in the heritage of different groups is shown also in the spermatogenesis of diploid males in *Habrobracon*. Here there is asynapsis; a cytoplasmic bud is given off, as in haploid males, and an equational division of the entire set of twenty chromosomes ensues, giving rise to two diploid sperms (Torvik-Greb, 1935). These may occasionally function in the production of triploid females. It is of interest to contrast the failure of reduction in the spermatogenesis of the diploid males of *Habrobracon* with its presence in the diploid spermatogenesis of the hermaphrodite *Icerya purchasi*. Possibly the general pattern of spermatogenesis in the Hymenoptera is more definitely fixed genetically, or it may be that since the hermaphrodite coccid is but little removed from the female, its diploid spermatogenesis takes on something of the character of oogenesis.

Regulation of meiosis in haploid males has, as we have just seen, been accomplished in a variety of ways. One or another of these methods must have been selected in the attainment of male haploidy from an assortment of diverse conditions depending in part, at least, upon the normal mode of the ancestral diploid stock.

Sex Determination

Zygogenetic back-cross sex determination

With the development of the Mendelian principles of heredity, it has been shown that sex determination, as a rule, is comparable to the "back-cross" of the heterozygous dominant to the recessive. Two general categories may be recognized,—the XY-male type and the WZ-female type.

Most animals and many dioecious plants belong to the XY-male type. In these one-half of the sperm cells receives the recessive factor X, the other half receives the dominant factor Y. All eggs receive the factor X from the homozygous recessive female, XX, in which crossing-over takes place. Cytological conditions corresponding to these factors are very diverse, especially in the male. The entire X-chromosome may segregate as a unit from the Y in meiosis, as in the fly *Drosophila*, or there may be crossing-over between portions of the X- and Y-chromosomes, as in man and in some fishes. In the latter case the factors X and Y correspond, not with entire chromosomes, but with those parts only that fail to cross over. The Y-chromosome may be larger than the X, it may be the same size and indistinguishable cytologically, or it may be smaller. There may be several small Y-chromosomes which segregate as a group from the X, or there may be no Y-chromosome. The factor Y then corresponds to the small chromosomes or to the absence of the X-chromosome.

The WZ-female type of sex determination is found in birds, in moths, and in some fishes. What has been said about the chromosomes in the XY-male type may be applied here also, but just in reverse as regards the sexes. The male has two Z-factors and is, therefore, recessive in a Mendelian sense. The female is heterozygous dominant, with W dominant over Z.

The sex of an individual is determined by the ratio existing between male-producing and female-producing genes. These sex genes may occur in the autosomes as well as in the sex chromosomes. They may be absent from one or the other of the sex chromosomes. In *Drosophila*, with sex genes absent from the Y, and X is predominantly female-producing and the autosomes predominantly male-producing. In the dioecious plant *Melandrium*, the Y is highly male-potent in genic content, the X is female-potent and very little if any sex potency has been located in the autosomes (Warmke and Blakeslee, 1940).

A single set of autosomes is designated A. In XY-male sex determination, the complete male formula is XY + 2A, the female formula 2X + 2A. However the sex genes may be arranged, there are more female-producing genes in the female, more male-producing genes in the male, and the difference in the ratio determines the sex. Since the autosomes are normally the same in the two sexes, they may be left out of the formula. Sex differentiation depends upon the type of sperm cell which fertilizes the egg.

In WZ-female sex determination, the male formula is 2Z + 2A, the female formula WZ + 2A, and the same principles outlined above apply, but in reverse as to the sexes.

"Protection" from natural selection exists in the heterozygote, so that one chromosome may degenerate, losing most of its genes, as has the Y in *Drosophila*, or becoming small in size or disappearing. Muller (1918) expressed this idea, stating that lethal changes and deleterious mutations as well as visible recessives "should be found to have arisen in any chromosome region that has been protected for a long time from the action of natural selection.... The Y chromosome is so protected by the X."

Geneticists often use the formulae of the cytologists, distinguishing XO males from XY males. These two formulae are, of course, inadequate to express the great variety of cytological conditions that exist in the XY-male type. Since it is usually unnecessary to express these differences in genetic formulae, I am, for the sake of simplicity, proposing to use the terms X- and W-factors as female differentiators, Y- and Z-factors as male differentiators. Linkage and crossing-over may then be expressed with the alleles X vs. Y and W vs. Z.

Chromosome constitution and, therefore, the sex of the individual, is usually determined at fertilization of the egg, but this may occur at other times, as, for example, during cleavage in certain zygogenetic animals. In the fly *Sciara* all zygotes begin as 3X + 2A but subsequent elimination of X's occurs so that the soma of the male becomes X + 2A and that of the female 2X + 2A (Metz, 1938). *Sciara* therefore belongs to the XY-male category.

In parthenogenesis, the chromosome constitution of the offspring is usually decided during meiosis. In the agamic generations of aphids, both X-chromosomes are, in general, retained in the egg so that females, 2X + 2A, are produced. However, one X-chromosome is regularly extruded from the male-producing parthenogenetic egg, leaving X + 2A.

Tychoparthenogenesis is usually haploid, with restoration of the diploid number by endomitotic doubling. The offspring, starting as haploids, are therefore homozygous both for sex and for other factors. With XY-male sex determination the offspring are, in general, females, 2X + 2A, from the X + A eggs laid by the 2X + 2A mothers. The rare exceptional males occurring here may be explained by failure of the X to double at the first cleavage. With WZ-female sex determination the offspring are males, 2Z + 2A from the Z + A eggs, and females, 2W + 2A from W + A eggs, in equal numbers. The exceptional composition of the females, WW instead of the usual WZ, will be discussed later.

Origin of parthenogenetic races and species

Parthenogenesis, as it exists in thelytokous races, rarely if ever is haploid. Parthenogamy from a polar body may occur as in *Lecanium* (Thomsen, 1929), but the more usual condition appears to be an advance of cleavage into meiosis so that an oocyte nucleus becomes the first cleavage nucleus. This advance may result in omission of synapsis, so that the nuclei resulting from the last oogonial division enter immediately upon cleavage. The diploid (or polyploid) group may then accumulate by mutation a considerable amount of heterozygosis. Obvious variation will then be limited to dominant changes, and different lines, lacking the possibility of crossing (amphimixis), will differ in many unseen (recessive) traits.

Vandel (1931a, 1936, 1937, 1940) regards tychoparthenogenesis (haploid) as the primitive type from which there has developed the normal and regular (diploid or polyploid) parthenogenesis of thelytokous races. Doubling of chromosome numbers, which occurs somatically in tychoparthenogenesis, is extended in thelytokous races to involve the germ track. Vandel (1936) makes comparisons in nuclear phenomena between tychoparthenogenesis, which he calls genotypic, and experimental parthenogenesis which is phenotypic, initiated by artificial means. Either type may be incomplete (rudimentary) or may result in an animal viable to maturity. He traces the origin of polyploidy in parthenogenetic races to a persistence and an extension of endomitosis or parthenogamy. He omits discussion of male haploidy, which he regards as a specialized problem insoluble from the data available to him.

In the evolution from the usual bisexual zygogenetic type of reproduction to the thelytoky of parthenogenetic races, there is elimination of the male and a tendency toward polyploidy. In the evolution of male haploidy, progression is in the reverse direction. Parthenogenesis produces males with reduced chromosomes. Since the race cannot consist entirely of males, a limit tends to be set to selection for this reduction, because the biparental females are necessarily diploid. There must also be established some genetic mechanism effecting physiological harmony of haploidy and diploidy in the same species. An answer to this problem is suggested in the nature of the sex differentiating factor which will be discussed below.

Thelytoky

Parthenogenetic races or species are, of course, female, thelytokous, except for the rare or spanandric males. The type of parthenogenesis is diploid (or polyploid), and the chromosome complement of the mother is passed on unchanged to the daughters.

Induced parthenogenesis may be either diploid or haploid. In the latter case mortality is very high, and the diploid number of chromosomes is usually restored in the few surviving individuals.

Let us first review parthenogenesis in some of the groups which are known to be of the XY-male type or are probably so. Here females are to be expected.

One impaternate rabbit, normal and presumably diploid, from induced parthenogenesis was raised to maturity by Pincus and Shapiro (1940), a female as expected from an XX mother.

Fankhauser's (1938) *Triton* from induced parthenogenesis, the only amphibian attaining the stage of sexual differentiation as a haploid, was female. It is not known whether salamanders are of the XY-male type.

The few impaternate frogs from experimental parthenogenesis reared to the stage of sexual differentiation were all diploid. They included individuals of both sexes and also a number of sex-intergrade types with considerable asymmetry. The frog is presumed to belong to the XY-male category, although there is no convincing cytological evidence, and genetic data are derived from race and species crosses and are not clear-cut. Kawamura (1939) who obtained only five frogs with testes among twenty-three impaternates, concludes that "the preponderance of females and the absence of typical males can be explained well by the theory of male digametism." The parthenogenetic origin of these frogs, with irregularities in chromosome regulation, may account for their tendency toward hermaphroditism, which was to some extent effective although they belonged to the sexually "differentiated" race.

Parthenogenesis is very rare in the two-winged flies, the Diptera. A few parthenogenetic races and species have been reported, especially in the Chironomidae (Sturtevant, 1923; Thienemann and Strenzke, 1940a, 1940b). Nothing is known of their cytology. It is of interest to note that paedogenesis, a type of parthenogenetic reproduction by larvae, also occurs in this same family. In haplo-diploid mosaics of *Drosophila*, Bridges (1930) showed the haploid region as well as the diploid to be female, as was to be expected from the known fact that Diptera are XY-male in type.

Parthenogenetic species have been recently reported in the Embioptera (Ross, 1940), the first parthenogenesis for this small order of neuropteroid insects, and in the Psocoptera (Badonnel, 1938), the "book-louse" order. Both species are known only as females.

Induced tychothelytoky has been shown in crickets (Ohmachi, 1929) and in termites (Light, 1944). Crickets, and probably also termites, the socialized relatives of cockroaches, are of the XY-male type.

Phasmids are of the XY-male type. There is an extensive literature from field studies and from breeding experiments showing geographic and constant thelytoky in many species (Cappe de Baillon and de Vichet, 1939, 1940). It is also certain that tychothelytoky occurs.

In the Saltatoria (jumping Orthoptera), parthenogenetic species appear to be rare. In the Tettigoniidae, Cappe de Baillon (1939) and Matthey (1941) have reported parthenogenetic species, with polyploidy probable from comparison of chromosome numbers in related forms.

Induced tychothelytoky has been shown in four species of the grouse locusts, Tetrigidae, in the extensive genetic experiments carried out by Nabours (1929, 1930). In one of these, *Apotettix eurycephalus*, among more than 5,000 impaternates bred to maturity, only thirteen were males. All were homozygous for numerous traits for which their mothers were heterozygous, indicating haploid parthenogenesis (King and Slipher, 1933). The homologous (sister) chromosomes in these impaternates tend to be approximated in the metaphase plates of cleavage in unfertilized eggs, while in fertilized eggs the homologues (members of paternal and maternal pairs) are widely separated (Robertson, 1930). Induced tychothelytoky also occurs in several Acrididae (Slifer and King, 1932; King and Slifer, 1934; Creighton, 1938). The meiotic process is normal, being unaffected by the absence of the sperm. The haploid set of early cleavage is doubled as development progresses, so that some, perhaps all, cells of the embryo become diploid. Development is successfully completed in few of the individuals, and these are females. The rare impaternate males in Nabours' grouse locusts may be readily accounted for by accidental loss of an X-chromosome or its failure to double along with the autosomes.

Insects of the order Lepidoptera, moths and butterflies, possess the WZ-female type of sex determination. Among moths of the family Psychidae and of the Lymantriid genus *Orgyia*, there are parthenogenetic species and geographic races which may be diploid or polyploid (Seiler and Schaeffer, 1941).

Astaurov (1940) has induced thelytoky by heat treatment in the silk-worm, *Bombyx mori*. The unfertilized eggs were immersed in water at 46.0° C. for eighteen minutes. About 500,000 caterpillars capable of transforming to adults were produced over the period from 1932–1937. Of 37,152 identified as to sex, 37,139 were females and only thirteen males. The great majority were of maternal phenotype and genotype. Cytological studies by Frolova showed that the eggs undergo a single division, presumably equational, and that the diploid number of chromosomes is retained. Eggs of impaternate females were subjected to treatment each generation for six successive generations. Tetraploid females also appeared, and these were perpetuated parthenogenetically by heat treatment. When tetraploid females were crossed with normal diploid males, there resulted sterile triploid males and females.

Deuterotoky

Several instances of tychodeuterotoky have been reported in different species of moths. The literature has been reviewed by Vandel (1931a) for these examples of infrequent facultative parthenogenesis, in which males and females are produced in approximately equal numbers.

T. L. Smith (1938), carrying out genetic experiments with x-ray mutant types in the wax moth *Galleria mellonella*, showed that while mated females lay from two hundred to one thousand eggs, which hatch in ten days, about ten per cent of unmated females show facultative parthenogenesis, and hatching requires several weeks. The impaternate offspring from a single female number from one to ten only, but these are normal in every way. Only seventy-nine attained an age in which sex was identified. There were forty males and thirty-nine females. When the mothers were heterozygous for recessive autosomal traits, the impaternate offspring were nineteen wild type and nine recessive.

According to genetic evidence, Lepidoptera have the WZ-female type of sex determination. Cytologically, females may be ZO or ZW. In the moth *Phragmatobia* there is one large Z- which segregates against two small W-chromosomes. Many species have no visibly differentiated sex chromosomes, and here it is presumed that the W-chromosome is equal in size to the Z. Chromosome numbers tend to be rather high in the Lepidoptera, and there is probably a considerable amount of distant phyletic polyploidy, in addition to the more recent cases in closely related species or varieties, in which one has double the number present in the other.

Explanation of the 1:1 sex ratio obtaining in the tychodeuterotoky of Lepidoptera apparently lies in the fact that it is haploid with subsequent doubling of the chromosome complex, and that the WW females, as well as the ZZ males, are viable (Seiler, 1923). It might have been expected that WW, which may be a homozygous deficiency, would be inviable and that all-male broods would result. Such have not been found, however, and we must attribute the viability of the females to vestigial polyploidy, with Z-factors duplicated and acting as autosomes (females Z′Z′ ZO, males Z′Z′ ZZ).

Sex determination in male haploidy

In all types of parthenogenesis other than male haploidy the principle of genic balance applies, so that sex determination *sensu stricto* is orthodox, however irregular may be the determination of chromosome distribution. This is true because the ratio of male-producing to female-producing genes is higher in males than in females, just as it is in "back-cross" sexual reproduction.

In haploid arrhenotoky, however, as it exists in the Hymenoptera and in the other groups mentioned above, sex determination has appeared to be fundamentally irreconcilable with generally accepted principles. This has been clearly stated by Bridges (1925). "To me, sex determination in the bee is the outstanding unsolved puzzle, although before the development of the idea of genic balance it seemed one of the clearest and simplest of cases. If it is true that the male is a haploid individual, then we would suppose that the diploid individual should likewise be a male, since the ratios among the sex-determining genes are not different in the two cases."

Three hypotheses were suggested to meet this difficulty before adequate genetic experiments had been carried out. One resorted to the cytoplasm, haven of cytogenetic theoreticians unable to make a better known port. The cytoplasm was supposed to transmit indefinitely a male tendency strong enough to dominate a single set of female-producing chromosomes, but dominated by the diploid set. This hypothesis disregarded the fact of regulation, assuming that the ratio of genic material to cytoplasm in azygotes was only half that in zygotes.

The second hypothesis placed sex differences in the Hymenoptera in the same category as those noted in different chromosomal types with multiples of the single complete set, in so-called euploid series. Such differences are seen in the rougher texture of eyes and larger size of triploid females of *Drosophila* and in the broader leaves of polyploid plants. However, the complicated sex differences found in insects are obviously of a very different order from these. This theory was elaborated into an algebraic sum hypothesis for male-determining and female-determining genes. When applies to the various sex and chromosomal types of *Drosophila*, it failed to fit the obvious relative intervals between them, as shown by Bridges (1925). This theory also ignored regulation and assumed a constant difference in quantity rather than in the rate of production of genic material, thus disregarding the factor of time.

According to the third hypothesis, it was supposed that the environment of the embryo might be different, that males were different because they had a different start in life than females, just as in a fern the gametophyte has the characters of a gametophyte because it develops from a spore, while the sporophyte is such because it begins in an archegonium. Thus, in the honey-bee there have been supposed to be two different types of eggs, a female-producing type which cannot develop unless fertilized (obligate zygogenesis) and a male-producing type which cannot be fertilized (obligate parthenogenesis). It is now generally recognized that, as regards the honey-bee, there is but a single type of egg, facultatively parthenogenetic.

Schmieder (1938), however, suggests that there may be two types of eggs in the chalcidoid *Melittobia chalybii* because of the "fact that the ratio of males to females (3:97), produced by normally mated females, is approximately the same as the ratio of males to unhatchable eggs, produced by females not so mated." These eggs might be female-producing if they were fertilized. However, "unmated females deposit only a very few eggs and of these only a small percentage undergoes development. It is therefore more practicable to study haploid development in eggs obtained from females mated with another species of *Melittobia*, since after such mating oviposition occurs often at a rate comparable to that occurring in normally mated females. The foreign sperm is generally observed as having entered the egg but actual syngamy seems never to occur, or, at least, never to yield viable zygotes. The small percentage of eggs that eventually hatches always produces haploid males of the maternal type." The unhatchability of the eggs fertilized by foreign sperm may be explained by a lethal effect of the foreign sperm, without the necessity of postulating the existence of two different types of eggs. However, if the ratio of males to the few unhatchable eggs laid by unmated females is also only three per cent, then these eggs may be of a different type from those developing into males. They may be unhatchable because unfertilized, or for some other reason, defective yolk, for example. It is stated of *Melittobia acasta* that virgin females lay only a few eggs which invariably develop into males.

In the ichneumonoid *Habrobracon juglandis* it is obvious that at least two-thirds and presumably all eggs are facultatively parthenogenetic. Hatchability may be as high as 98 per cent and viability to the adult stage as high as 90 per cent, whether the females are mated or not. Since two-thirds or more of the offspring from mated females are females, at least this proportion of the eggs which produce males, if unfertilized, would produce females if fertilized.

Results from genetic experiments bearing upon the problem of male haploidy will now be presented.

In the ichneumonoid wasp *Habrobracon juglandis* (*Ashmead*), investigated by the writer and his co-workers, a large number of recessive mutant traits has been obtained, and crosses have been made in various ways to test the principles of heredity. Unmated females heterozygous for various traits produce haploid males segregating in azygotic (approximating gametic) ratios. Linkage tests thus made show that maps are very long in crossover units. On this account, despite much work extending over several years, there is as yet no approximation of linkage groups to the number ten, corresponding to the haploid set of chromosomes.

Recessive females crossed with dominant males produce recessive haploid sons and dominant heterozygous daughters, as expected according to Dzierzon's Law, but if the parents come from the same general stock, then there are also regularly produced diploid biparental males, which resemble their sisters in showing all the dominant traits inherited from both parents, but which are in no way intersexual. They are, however, of low viability and almost sterile. Their sperms are diploid, and consequently their few daughters are triploid. Diploid males are separable from their haploid brothers, not only in showing paternal traits, but also, with some difficulty, by slight differences in proportion of bodily structures and by the larger size of their cells. These are, in fact, much larger than the cells of diploid females. Triploid females, the daughters of diploid males, have cells even larger than diploid females, and haploid males average in cell size almost as large as diploid females (B. R. Speicher, 1935). It appears, then, that while increase in number of chromosome sets increases cell size, maleness as such is an even more effective factor.

Sex determination has been shown to depend upon a series of multiple alleles, of which nine have thus far been identified (Whiting, 1940a, 1943). These are designated *xa*, *xb*, etc., to *xi*. Any heterozygote (diploid), *xa/xb*, *xa/xc*, *xc/xd*, etc., is female; any azygote (haploid), *xa*, *xb*, *xc*, etc., or any homozygote (diploid), *xa/xa*, *xb/xb*, etc., is male. Each member of the allelic series is regarded, not as a single gene, but as a chromosome segment, perhaps very long (to speak in relative terms, because the chromosomes are all very small) and containing many different genes which do not cross over. Thus the allele or segment designated *xa* might have the genes + *Fa mb* + *mc* + etc., *xb* might have *ma* + + *Fb mc* + etc., and *xc* might have *ma* + *mb* + + *Fc* etc.

From these formulae it may be seen that any heterozygote will show more of the dominant traits determined by the female-producing genes, *Fa*, *Fb*, *Fc*, etc., and that any homozygote or azygote will show more of the recessive traits determined by the male-producing genes, *ma*, *mb*, *mc*, etc. Sex determination is, therefore, complementary, with females of the different genotypes being heterozygous (diploid) dominants for many of the genes, while the males are homozygous (diploid) or azygous (haploid) recessives. Genes for secondary as well as for primary sex characters must be located within this segment. The longer antennae, the larger ocelli, the slightly larger eyes, and the weaker sclerotization of the abdomen of the male must be dependent upon such genes, which in the aggregate are also recessive.

The complementary character of sex determination is shown by certain males which are mosaic for various mutant traits (Whiting, Greb, and Speicher, 1934). Haploid mosaic males occur in a small but variable proportion, less than one per cent, of the offspring of heterozygous females. If a female (black-eyed double dominant) is heterozygous for two different white eye colors, called white, *wh*, and ivory, *oi*, respectively, a son may be produced having the eyes in part white, in part ivory. These two eye colors are normally indistinguishable, but ivory is non-autonomous in mosaics, so that a soaking-through effect takes place from the non-ivory tissue. The complementary action of the two dominant alleles, non-white and non-ivory, then causes a black line in the ivory region edging the white. This black region is "physiologically" double dominant, but genetically ivory. Similarly, in the region of the genitalia of a proportion of mosaic males there are developed small-sized "female" reproductive appendages, indicating a complementary action of dominant female genes in the different sex alleles characterizing the two different types of tissue of the mosaic male. The influence appears to be unidirectional, as if, for example, *xa* affected *xb* but not the reverse. This has, however, not been checked with the different alleles of the series. It was this complementary action in these "gynandroid" males (resembling gynanders) that first gave the hint of complementary sex factors that led to the formulation of complementary sex determination.

Sex determination is, in a sense, polygenic, but because of no crossing-over within the segment, the various groups of genes act as a single series of allelic factors. Just as the many sex-producing genes distributed along the X-chromosome of *Drosophila* segregate as a unit from the Y without crossing-over, so the dominant female-producing genes and the recessive male-producing genes of the *x*-factor in *Habrobracon* segregate without crossing-over from their homologues. Males, as determined by the various alleles (whether azygous or homozygous), or females as determined by any of the heterozygous combinations, are always phenotypically similar.

Whether the sex-alleles ever mutate has not been established with certainty. They appear to be very stable. Extensive breeding within a two-allele stock has resulted in two-allele fraternities almost exclusively, as evidenced by the presence of diploid males. With certain very rare exceptions, the fraternities lacking diploid males are small, so that the lack is evidently due to error of sampling. The rare exceptions, which were not adequately tested, may have been due to contamination, though this is unlikely, or to some combination of factors reducing diploid male viability, or to mutation in a sex allele itself.

In linkage tests, the *x*-factor acts as a single gene, occupying a point on the linkage map. It has been shown to lie near the center of the left arm of a linkage group which is about five hundred crossover units in length. Since no interference occurs across a region approximately central, it may be supposed that the centromere is median.

The method of making a linkage test with the sex-factor may be illustrated by a single example. The mutant gene fused, *fu*, lies about ten units to the right of *x*. An orange-eyed, *o*, female heterozygous for fused, $\frac{o\ xa\ +}{o\ xb\ fu}$, is crossed with a black-eyed fused male, + *xb fu*. The orange-eyed sons are haploid from unfertilized eggs and are fused and non-fused in equal numbers. Sex linkage is not determinable among these because *xa* males and *xb* males are similar. The black-eyes zygous diploid or biparental offspring, *o*/+, are either fused or non-fused and either males or females. From the ratio of the different combinations, the percentage of crossovers may be determined. In the example given, the non-crossover offspring will be $\frac{xa\ +}{xb\ fu}$ or non-fused females, and $\frac{xb\ fu}{xb\ fu}$ or fused males; the crossovers, averaging in this case 10 per cent, will be $\frac{xb\ +}{xb\ fu}$ or non-fused males, and $\frac{xa\ fu}{xb\ fu}$ or fused females. This is called a two-allele cross.

In crosses involving three sex-alleles, sex-linkage cannot be determined, because all the zygous offspring are heterozygous for x and are therefore female. $xa/xb \times xc$ gives xa/xc, xb/xc. Fecundity is higher here, and the ratio of females to haploid males is doubled, because the poorly viable diploid males are replaced by females. In this case, if the cross is made between a female heterozygous for fused and a fused male, fused and non-fused females are in equal numbers.

Three kinds of fraternities from heterozygous females by fused males are therefore distinguishable as follows:—

	Females $\frac{\text{non-fused}}{\text{fused}}$	Diploid males $\frac{\text{non-fused}}{\text{fused}}$	Haploid males $\frac{\text{non-fused}}{\text{fused}}$
(1) two-allele. . . .	9/1	1/9	1/1
(2) two-allele .	1/9	9/1	1/1
(3) three-allele. . ..	1/1	0	1/1

Before the multiple allele principle was demonstrated, two different hypotheses, now discarded, were suggested to explain the lack of diploid males in three-allele fraternities. These were differential mutaration, and multiple independently segregating factors (Whiting, 1935).

Habrobracon is an arrhenotokous species, but in combinations of certain stocks unmated females produce a small proportion of diploid daughters in addition to their haploid sons. These impaternate daughters are either heterozygous or homozygous for genes for which their mothers were heterozygous. Female $+/a$ produces impaternate daughters in the ratio: $1\ +/+$, $2\ +/a$, $1\ a/a$. It was at first supposed that suppression of meiosis, or parthenogamy from a polar nucleus, might cause their appearance (K. G. Speicher, 1934) but cytological work later showed twenty tetrads, the diploid number, in the first oocyte mitosis (Speicher and Speicher, 1938). Two meiotic divisions would then leave the diploid number of monads in the egg nucleus. If the homologues contained different sex-alleles, a female would result. The fact that the heterozygotes for a mutant gene are equal to the homozygotes rather than twice as numerous indicates that the genes, $A\ A\ a\ a$, assort as two pairs, Aa and Aa, rather than at random. This is to be interpreted as meaning that synapsis is initiated in two oocyte I groups of chromosomes which remain separate, and each of which contains both a haploid paternal and a haploid maternal set. The bivalents are therefore paternal-maternal, none being paternal-paternal or maternal-maternal.

If the mother is heterozygous for a sex-linked gene, the 1:2:1 ratio of impaternate females does not hold. Thus when the mother is heterozygous for fused, most of her impaternate daughters are also heterozygous. Most of the homozygotes should be diploid males (Whiting and Speicher, 1935). This example of tychothelytoky in an arrhenotokous species is of interest as showing a possible step toward a thelytokous race.

It will now be of interest to examine forms with haploid arrhenotoky other than *Habrobracon juglandis*, and it will be pertinent to inquire whether there is positive evidence indicating that the *Habrobracon* scheme cannot be universally applied. We may have the possibility of some complementary scheme not involving multiple alleles. Reproductive economy might be low with wastage of fifty per cent of the fertilized eggs (diploid males), as in two-allele crosses of *Habrobracon juglandis*, or good reproductive economy might be attained by some sort of non-randomness in fertilization, by independent pairs of multiple factors, or by some other means to assure that all fertilized eggs should develop into females. Cytologic and breeding data are, unfortunately, indecisive, and genetic evidence is very meager.

We may first consider data from other Hymenoptera and later review the other groups that show haploid arrhenotoky. Two species of *Habrobracon* other than *H. juglandis* have been studied to some extent. In *H. brevicornis*, aberrant males were found (Whiting, and Whiting, 1927) similar to the gynandroid males in *H. juglandis* which gave the hint for complementary sex inheritance. No genetic data were available, but it is probable that these were also gynandroid sex mosaics. B. R. and K. G. Speicher (1940), using a recessive mutation in the same species (rough, similar to rough in *H. juglandis*), obtained from rough females by wild type males, 51 wild type females, 172 rough males, and 34 wild type males. The wild type sons were diploid, as shown by cytologic study, having twenty chromosomes in the spermatocytes instead of ten, the number found in haploid males. These observations may be taken to indicate complementary inheritance.

More extensive data are available for *H. pectinophorae* from the work of Inaba (1939). Diploid males were obtained, identified as in *H. juglandis*, by crossing recessive females with white eyes or with curved wings to wild-type males. The ratio of females to haploid males was higher in fraternities without diploid males, suggesting three-alleles. Triploid females were obtained, sired by diploid males. Cytological study showed conditions, in general, similar to those in *H. juglandis*, but the chromosomes were evidently somewhat larger and had different spindle fiber positions. Chromosome numbers were as in *H. juglandis*, ten in haploid males, twenty in diploid males and in females, and thirty in triploid females.

These data indicate that cytogenetic conditions in the different *Habrobracon* species are very similar.

In the chalcidoid *Pteromalus puparum*, Dozorceva 1936a, b, c, d; Whiting, 1940b) found a sex-linked trait, red eyes. No fraternities were reported from red-eyes females by wild-type males, such tests for diploid males being lacking. Heterozygous females by red males produced three kinds of fraternities, those with a marked excess of red females, those with a marked deficiency, and those approximating equality. Presumably the first two are from two-allele crosses and the last from three-allele. It is claimed by Dozorceva that there are two types of males, in one of which the sex chromosome is much shorter than in the other, and that females are digametic. As noted above, however, her genetic evidence suggests triple allelels, *xa*, *xb*, *xc*, so that the conditions may be similar to those in *Habrobracon*. B. R. Speicher (unpublished), after examination of *Pteromalus puparum* collected on Long Island, N. Y., was unable to confirm the cytological conditions picture by Dozorceva in the Russian material.

The egg parasite *Telenomus fariai* (Lima), a scelionid wasp of the superfamily Proctotrypoidea, has been investigated cytologically by Dreyfus and Breuer (1944). Daughters and sons of the same mother copulate before leaving the host egg shell, so that there is normally very close inbreeding. Unmated females produce only males. Mated females produce bisexual broods, with females in excess of males. Females have twenty chromosomes, males ten. No diploid males were found. According to the authors, one of the large pairs of chromosomes consists of a V-shaped and a J-shaped member. Males are all haploid, and spermatogonia all show the V. However, the large chromosome that appears in the equal first spermatocyte division is a J. The last spermatogonial division is unequal cytoplasmically. The smaller daughter cell degenerates, while the larger becomes the first spermatocyte. It is assumed that in this division one arm of the V breaks and that the spermatocyte therefore receives a J. The second spermatocyte division is abortive, with a cytoplasmic bud pinched off. Sperms are then all J-bearing. It is further assumed that maturation of the egg is differential, so that the V is always retained. All fertilized eggs then give rise to females, all unfertilized to males. It would be of much interest to have genetic work on *Telenomus* to check with the cytological findings.

Haploidy of the azygous male

The complementary principle of sex determination answers the question, "Why is the haploid a male?" We may now consider the problem, "Why is the male a haploid?" Somatic haploidy has been questioned with respect to the males in many of the arrhenotokous groups. Evidence based on cleavage nuclei is regarded as inadequate (Vandel, 1931a; Schrader and Hughes-Schrader, 1931). We have seen that the drone bee is somatically diploid (in part polyploid) and that this "somatic" diploidy involves most of the germ track.

The difference between the azygote of tychoparthenogenesis and the azygote of haploid arrhenotoky lies in the fact that the former has the diploid type of gametocytes while the latter has the haploid type. The haploid type has become so fixed genetically in the Hymenoptera that spermatogonial diploidy, whether determined by male biparentalism, as in the diploid males of *Habrobracon*, or by regulative doubling, as in the drone honey-bee, fails to result, in the spermatocytes, in the diploid type of mieosis that would produce haploid sperms. The sperms produced are therefore diploid. There is, however, a significant difference in the two cases. Diploid *Habrobracon* males have triploid daughters, because their diploid sperms unite with reduced haploid eggs. The diploidy of the biparental males is "genetic," since their offspring are different from the offspring of haploid males. Diploid drone bees have tetraploid daughters, because the reduced eggs are diploid. Nevertheless, in the bee, eight remains the gametic number because reduction to eight takes place in the oocytes. The diploid drone, therefore, breeds as a haploid although he produces diploid sperms, and the tetraploid queen breeds as a diploid, although she produces diploid instead of haploid eggs. Eight dyads go to each pole in anaphase and oocyte I and there are eight "monads" in telophase of oocyte II. Whether these "monads" have already become dyads through regulative splitting, and just when the dyads divide to produce a diploid female pronucleus, is a problem for cytological technique and observation. Although somatic diploidy is here extended into the germ track, it does not produce genetic diploidy. If we had been studying genetics rather than cytology, we would not have been aware of this regulative splitting.

The "somatic" diploidy of the drone bee I regard as a secondary type of regulation, subsequent to and probably supplanting the regulation in size of the haploid chromosomes that are seen at least in cleavage and in spermatogenesis of most males in arrhenotokous groups. The drone bee has devised a mechanism extending diploidy into the germ track without surrendering the haploid type of spermatogenesis and his capacity to breed as a haploid. The honey-bee is thus admirably adapted through numerical regulation, so that chromosome numbers in corresponding tissues in males and females are the same. Biparental diploid males of *Habrobracon*, however, are a waste product, of low viability, probably because of their excessively large cells, and producing diploid sperms which are rarely able to fertilize the eggs.

The question asked at the beginning of this section, "Why is the male a haploid?" may be reformulated to read "Why have the males in the groups showing haploid arrhenotoky evolved a haploid type of spermatogenesis instead of retaining the diploid type of the ancestral zygogenetic groups from which they came?"

An answer to this question, which must necessarily be hypothetical, and even somewhat speculative, may be formulated as follows.

The diploid impaternates of tychoparthenogenesis undergo, at some point in their development, delay in cytokinesis relative to chromosome splitting, and thus they become diploid. This may involve a certain disharmony in rhythm between cell body and nucleus. The males of haploid arrhenotoky have had ample time, in the course of evolution, to acquire genes located in the sex differentiating segments, *xa*, *xb*, *xc*, etc., which retard chromosome division relative to chromosome growth. Since these genes are recessive, they do not affect the females (sex heterozygotes) but only the males. Haploidy of the azygous males thus attains regulation of the nucleoplasmic ratio without introducing disharmony between division of nucleus and of cell. Evolution may here have found a more satisfactory solution of the problem of regulation than occurs as an immediate solution in tychoparthenogenesis. Diploid impaternate female grasshoppers, produced by haploid thelytoky, if isolated for many generations, should be found to have advanced cleavage into meiosis so that the oocyte nuclei would become the first cleavage nuclei. Parthenogenesis would then become diploid. Continued endomitosis would result in polyploidy. This is the evolutionary course of azygosis in the female.

The evolutionary course of azygosis in the male must necessarily be different. The azygotic males of haploid arrhenotoky are selected to breed as haploids. This fact sets a limit to their somatic polyploidy.

ORIGIN AND DISTRIBUTION OF MALE HAPLOIDY

Having discussed the various problems involved in the attainment of male haploidy, we may now consider theoretical possibilities concerning the manner in which this mode of reproduction may have arisen. We have seen that parthenogenetic (female) races and species occur with greater or less frequency in diverse groups. This type of constant parthenogenesis has evidently arisen independently many times. It tends toward polyploidy and, as Vandel (1936) suggests, it probably originates from tychothelytoky. Male haploidy, on the other hand, has evidently become established very infrequently, despite the fact that it is a highly successful mode of reproduction possessing the advantages of amphimixis and involving very large taxonomic groups.

The Chromosome Degeneration Hypothesis

Schrader and Hughes-Schrader (1931) have presented a theory of the attainment of male haploidy based on the gradual inactivation or degeneration of one of the haploid groups of chromosomes. This theory attempts to answer the problems of the acquisition of viability in the haploid state and of the regulation of meiosis in the haploid male.

The theory is based largely on work with the homopteran family Coccidae, the scale insects. In this family there exist diverse cytogenetic conditions which, it is suggested, represent "both beginning and end stages in the establishment of haploidy." In the genera *Llaveia* and *Protortonia* both sexes are invariably diploid, while in *Icerya* and related genera the females are diploid from fertilized eggs, the males haploid from unfertilized eggs. Intermediate stages may therefore be expected, but in no case has a haploid individual been found within the diploid species. However, there is a series of chromosomal conditions of the diploid males themselves which is supposed to represent intermediate stages in the acquisition of haploid male viability. "The basic phenomenon is a gradual degeneration of one haploid set of chromosomes in the male; the process is reflected chiefly in the behavior of the chromosomes during meiosis, but in its late stages the soma also is affected."

The "degeneration" begins in *Llaveia bouvari*, in which about five per cent of the spermatocytes show asynapsis of one autosome pair, while in the remainder pairing is normal. In *Protortonia primitiva,* no pairing of the ordinary sort occurs; asynapsis affects both autosome pairs. There is no evidence for any selective assortment in segregation.

In *Gossyparia spuria,* one haploid set shows marked heteropycnosis, condensing prior to the other set, segregating selectively together and forming a non-functional sperm. The somatic cells, as well, show clumping of this set which appears first during the late blastula stage of the males. There are no heterochromosomes, but males and females are produced by each mother from zygotes which are not morphologically separable in chromosome content. Conditions are apparently similar in the genera *Pseudococcus, Lecanium,* and *Phenococcus.* In *Phenococcus acericola* (Hughes-Schrader, 1935) the later stages, showing disintegration of the condensed group, are especially clear. It is concluded that "a physiological haploidy seems to be in progress of evolution through the inactivation of one of the haploid sets of chromosomes in the male line."

Finally, in the iceryine species, the morphological haploidy of the males is completely established.

In the females of all species studied meiosis is of the orthodox type with normal synapsis, with no heterochromosomes, and with two divisions resulting in haploid nuclei.

It is stated that "this scheme attempts no expression of the phylogenetic relations of the various coccid species involved" but "is rather to be interpreted to the effect that some such development as we have traced is taking place in different groups of coccids, but evidently at different rates, and probably in different ways, in different groups.'

The writer doubts that the three cytological departures from orthodox conditions demonstrated in the male coccids-asynapsis, heteropycnotic clumping, and haploid parthenogenesis—are related phenomena.

Asynapsis, involving failure of crossing-over, is of frequent occurrence in other forms. There may later be contact of homologues, a "touch-and-go pairing," so that normal segregation occurs and inviable zygotic combinations are thus avoided, or, as in the asynaptic mutant type in maize (Beadle, 1930), even this brief approximation of homologues may be lacking and chromosomes may be assorted irregularly, so that few gametes contain the haploid set. In none of these cases does there appear to be any association between asynapsis and chromosome degeneration.

There likewise appears to be no association between haploid parthenogenesis and chromosome degeneration. No specific set of chromosomes is "lost" in the formation of haploid males, since any of the possible combinations of chromosomes (or of genes) present in the diploid mother may be transmitted to her haploid sons.

The degenerative processes noted in the male coccids of the Gossyparia type may be compared with conditions in the fly *Sciara* (Metz, 1938). Here a complete and perfectly normal chromosome set received by a male from his mother will,if transmitted to his son, be lost in the monocentric mitosis of the spermatocytes of his son. Just what chromosomes, whether paternal or maternal, are lost in *Gossyparia* is not known, for no genetic factors have been followed to tag them as has been done in *Sciara.*

In *Sciara* all zygotes are similar at the beginning, and sex is determined by differential loss of sex chromosomes in cleavage. This loss depends upon the genetic constitution of the mother which may be a male-producer or a female producer; or, in certain races, both sexes may occur in the same brood. Comparison may further be made with conditions in the isopod crustacean *Trichoniscus provisorius* (Vandel, 1938), in which, as in *Sciara,* there are (monogenic) races with unisexual broods having female-producing (thelygenic) females and male-producing (arrhenogenic) females, and there are (deuterogenic) races with bisexual broods.

(The terms used here indicating sex of offspring imply a special type of zygogenetic reproduction rather than parthenogenetic). Whether in *Trichoniscus* there is chromosome elimination or clumping in cleavage is not indicated, but the breeding data here suggest interesting comparisons with the cytological and breeding data on *Gossyparia* and with the cytogenetic conditions in *Sciara.* Evidence suggests that certain other invertebrates may likewise possess a comparable mode of zygogenetic reproduction showing aberrant sex ratios.

Review of Groups Showing Male Haploidy

In the introductory part of this paper there are listed seven groups of animals with haploid males. The Hymenoptera have already been discussed in some detail, and it is now in order to review the others because of their implications for the evolution of male haploidy.

Iceryini

In the iceryine coccids cytological conditions are very clear. The females have four chromosomes, the males two (Hughes-Schrader, 1930). No diploid males have been found. Unmated females produce males only, mated females produce both males and females. In the cottony cushion scale *Icerya purchasi* (Hughes-Schrader, 1927) true females are lacking, but their place is taken by hermaphrodites which presumably evolved from females. These hermaphrodites may produce further hermaphrodites, either by self-fertilization or by mating with males, but since males are infrequent and the eggs are developed in such a way that they are surrounded by sperms from the same individual, self-fertilization is the rule. According to the complementary hypothesis, only two sex alleles would be involved, and the alternatives are presented of considerable reproductive wastage or some type of non-randomness in distribution of sex factors. "Coincident with or slightly before the first appearance of haploid nuclei in the hermaphrodite gonad, degeneration of certain germ cell nuclei occurs" (Hughes-Schrader, 1927). Whether this is in any way selective is not clear. There is apparently no marked mortality of eggs subsequent to fertilization, but the possibility is not excluded that death of the homozygotes, diploid males, may occur at some post-embryonic stage. This highly successful species may be tending, through hermaphroditism and self-fertilization, toward the eventual complete elimination of males and may be getting on very well in spite of a possible wastage of fifty percent of its eggs.

Haploid males have not been found in other groups of coccids, among which the species are either zygogenetic or parthenogenetic (female). Sex determination in some groups (*Gossyparia*, etc.) may be of the *Sciara* type. In others (*Llaveia*, etc.) it is of the usual XY-male backcross type (Schrader and Hughes-Schrader, 1931).

Aleurodidae

"White-flies" of the homopteran family Aleurodidae are pests in greenhouses and in fruit orchards. The group has been much neglected by taxonomists, and it is probable that the majority of the species is as yet undescribed. In many species males are not known. Zygogenetic species have not been found. *Aleurotulus nephrolepidis* (Thomsen, 1927) is purely thelytokous. Morrill and Back (1911) state that virgin females of *Dialeurodes citri*, the citrus white-fly of the southern United States, produce males only. Thomsen (1927) reports that in *Aleurodes proletella* there is arrhenotoky, and that mated females produce both males and females. All eggs give off two polar bodies, and the unfertilized remain haploid.

In *Trialeurodes vaporariorum* (Schrader, 1920, 1926; Thomsen, 1927) there are two races. An arrhenotokous race occurs in America, in England, and in Denmark. A race reproducing by indefinite thelytoky and with spanandric males occurs in England and in Denmark. Thelytokous females may be mated with males of the arrhenotokous race or with the spanandric males, but it is supposed that the eggs are not fertilized. Maturation is apparently the same in the eggs of both races, with two polar bodies given off and chromosome number reduced from twenty-two to eleven. In the thelytokous race the eleven chromosomes of the reduced egg nucleus probably divide before the first cleavage giving the diploid number, for in the two-nucleus stage of cleavage the chromosome number is twenty-two. Regulation of this type is theoretically reconcilable with the *Habrobracon* principles of sex determination, if it be assumed that the thelytokous race differs from the bisexual due to a chromosomal rearrangement. As I have stated in a previous publication (Whiting, 1943), "homozygous females might be produced if x were duplicated either by translocation or by unequal crossing-over so that $xa/xb + 2A$ would become $xa\,xb/xa\,xb + 2A$. Theoretically, haploid females $xa\,xb + 1A$ would then be possible. That such have not been found is not surprising, however, since thelytokous forms tend to become polyploid rather than haploid."

Micromalthus

Among the beetles there are several thelytokous species and races, especially in the Curculionidae (Székessy, 1937; Milliron, 1939; Suomalainen, 1940). Most of these are polyploid. I have found no reference to tychoparthenogenesis in the Coleoptera. Since beetles are of the XY-male type, we might expect haploids to be female.

In males of the aberrant beetle *Micromalthus debilis*, however, Scott (1936) was able to establish somatic haploidy from examination of blastoderm nuclei and tissue of the sternal gland. *Micromalthus*, the only representative of the family-Micromalthidae, is the only example of haploidy reported in beetles and also the only beetle showing paedogenesis. Spermatogonial divisions are regular, showing ten chromosomes. The aberrant spermatocytes have already been mentioned. The life history is complex (Scott, 1938), with hypermetamorphic larval stages and with paedogenesis suggesting the cecidomyid flies *Miastor* and *Oligarces*. Normally the larval mother of the adult male deposits a single egg, from which there hatches a "metrophagus" larva. This larva, after devouring its mother, pupates and then ecloses as an adult. Scott (1941) was able to show that if the egg is removed before it hatches, the larval mother will then produce female offspring viviparously. Sex is therefore determined in the process of oogenesis. Normally, females are produced viviparously by paedogenetic larvae. Cleavage nuclei in female-producing eggs have twenty chromosomes. Continuous paedogenesis apparently maintains the species, and it is not known whether the adults reproduce.

No sex chromosomes are differentiated cytologically. The diploids, larvae and the adult female, may be heterozygous for sex as in *Habrobracon*, xa/xb. Haploid parthenogenesis would then produce males, xa and xb.

Thysanoptera

Minute insects known as thrips belong to the Thysanoptera, an order of uncertain affinities. Thelytoky occurs as the usual mode of reproduction in several species, which are members of different families in both suborders. Collections show wide deviations in sex ratios of the bisexual species and differences occur in different seasons of the year suggesting arrhenotoky. Of two species of *Anthothrips*, *niger* is thelytokous, ***verbasci*** is arrhenotokous, as shown by breeding tests (Shull, 1917), and collections indicate that *Chirothrips manicatus* is arrhenotokous. Breeding tests have likewise shown arrhenotoky in *Frankliniella insularis* (Davidson and Bald, 1931). There is some evidence that bisexual generations may alternate with thelytokous in *Physopus pallipes*, but Vandel (1931a) considers that two different races may exist in this species. There seems to be no evidence that males are produced bisexually, and since arrhenotokous types occur in both suborders, parthenogenesis may exist in all species of the order, with some thelytokous, others arrhenotokous, and with still others having racial types differing in this respect.

Trochelminthes

With the exception of a single family, the Seisonidae, which are marine parasites on the crustacean *Nabalia*, the males of rotifers appear at certain periods only and are presumably impaternate and haploid. The phylum Trochelminthes is characterized by irregular heterogony or alternation of generations (Shull, 1929; Whitney, 1929). Females are of two types, gamic and agamic. All eggs produced by agamic females give rise to females parthenogenetically and cannot be fertilized even though mating may take place. Males appear at certain times and much work has been done in attempts to determine the various causes of male production. In addition to genetic differences in strain or species, factors are temperature, nourishment, and chemical composition of the water. Since agamic females cannot produce males, these factors do not cause the production of males directly, but rather the production of gamic females. If gamic females do not mate, their eggs develop immediately into males by haploid parthenogenesis. Fertilized eggs do not develop for a considerable time. They accumulate reserves of nourishment and a thick shell to tide the species over unfavorable conditions. Eventually they give rise to females, which are always agamic, but the next generation may consist of gamic and agamic females. Eggs of agamic females give off but one polar body and produce females by diploid parthenogenesis. Eggs of gamic females form two polar bodies whether they are fertilized or not.

Some rotifers have but one sexual period a year, usually in the spring, others have one in the spring and a second in the fall, while still others have many sexual periods, the number of which may vary according to locality. Males are unknown in the Bdelloida and in species of several other groups, so that these forms reproduce by constant thelytoky.

The more primitive rotifers are crawling types, thus showing some resemblance to their possible ancestors, the Turbellarians (Wesenberg-Lund, 1923, 1930). In these rotifers the males are as large in size as the females. Evolution seems to have been in the direction of planktonic habit and of smaller size of males, with correspondingly greater numbers produced in the sexual period. There is no parasitism of the male on the female, but structural degeneration is carried so far that the male may be nothing but a sperm sac, surrounded by protoplasm bearing a tuft of cilia which enables it to reach the female. The sperms in this case are already fully formed before the male emerges from the egg, and the male mates immediately after hatching. Hermaphroditism is lacking in the phylum. In the family Notommatidae, regarded as the primitive type from which most, if not all, of the other families may be derived, very few males are known, but these are in size similar to the females.

The Seisonidae, mentioned above, are said to depart from the rotifer type, in that males are as abundant as females and can be obtained at all seasons. They are supposed to be produced bisexually, and it is stated that there is no parthenogenesis in the group. The single reference to spermatogenesis (Illgen, 1914) does not indicate whether the males are actually diploid and produced bisexually. If this be true, it suggests that a group which has attained haploid arrhenotoky may revert to the usual method of sexual reproduction. However, the family is somewhat isolated taxonomically, is primitive in the sense that the males are equal in size to the females, so that its origin may be separate from that of the other rotifers. A third possibility is that this family has retained haploidy but has given up heterogony. Without breeding tests or cytological study of the spermatocytes, it cannot be stated that Dzierzon's Law does not apply to this group.

Acarina

The Acarina, mites and ticks, are the only arachnids in which parthenogenesis has been proved with certainty. Sokoloff (1934) investigated spermatogenesis in six species of the Parasitidae (Gamasidae) showing tetrads with normal division. André (1935) discusses this family and concludes that, despite several supposed cases of parthenogenesis (thelytoky). none has been proved.

André (1935) also discusses the ticks (Ixodoidea) and concludes that thelytoky has been established only in *Amblyomma*. In *Hyalomma aegyptium*, Tuzet and Millot (1937) show a large body in the first spermatocyte which they interpret as a heterochromosome. It is probably a sex chromosome but is not illustrated in their drawing of spermatocyte II and should be further investigated. In *Argas columbarum*, Oppermann (1935) shows a large XY pair, in addition to twenty-four autosomes, in the spermatogonia. The autosomes synapse to form twelve tetrads which divide in the usual manner. Division of spermatocyte I is equational for XY, and division of spermatocyte II is reductional. In addition to twenty-four autosomes, the two X-chromosomes are shown in the oogonia.

André (1935) regards the observations made on *Syringobia chelopus* of the Sarcoptidae as inexact and as not establishing thelytoky. In the Cheyletidae, there have been several supposed cases, but only one proven. *Cheyletus eruditus* Schr. is regarded as thelytokous, but Cooper (1937) states that the possibility of its being a self-fertilizing hermaphrodite has not been excluded, and the same applies also to the tick *Amblyomma dissimile* Koch.

Evidence for arrhenotoky in mites is much more convincing. Putnam (1939) states that unmated females of the plum nursery mite (*Phyllocoptes fockeui*), of the Eriophyidae, produce males only. Pätau (1934, 1936) has shown that the grain itch mite *Pediculoides ventricosus* is arrhenotokous, with three chromosomes in the spermatogonia. He has investigated cytological conditions in the egg. The three bivalent chromosomes of the oocyte were followed from pachytene through the growth stage and appear as either rod or ring tetrads in metaphase. There are two meiotic divisions. In early cleavage telophases, the chromosomes form separate karyomers. Pätau discusses the application of the *Habrobracon* scheme of sex determination, but at the time his paper was written he did not have available the multiple allele principle.

Cooper (1937, 1939) has shown that the grass mite, *Pediculopsis graminum*, is arrhenotokous. His cytological studies revealed conditions very similar to those in *Pediculoides*, with three as the haploid number, six as the diploid, and with karyomeres formed by chromosomes in cleavage. *Pediculoides* and *Pediculopsis* are very closely related genera of the family Tarsonemidae.

Schrader (1923) showed arrhenotoky in the "red spider" *Tetranychus bimaculatus*, with three chromosomes in spermatogenesis, and with three pairs of chromosomes in the female forming tetrads in oocyte I. Cleavage is shown in the unfertilized egg, with three chromosomes, and in the fertilized, with six that form karyomerites in the resting stage. Other species of Tetranychidae mentioned as arrhenotokous are *Tetranychus telarius*, *lintearius*, and *ulicis*.

The Acarina are exceedingly diversified in modes of life, structure, and developmental conditions. There is great disparity in the method of grouping the various families, so that selected species may be far separated or not, according to the system adopted. If the arrangement suggested by Ewing (1934) be followed, placing the Parasitoidea and the Ixodoidea together in the Mesostigmata, which is one of the twelve suborders, then the forms reported as zygogenetic, having normally diploid biparental males, will be grouped together. How many other mites are also zygogenetic, and how widely spread is arrhenotoky, remains to be investigated. Possibly arrhenotoky has arisen and become established but once in the order, which may suggest that the primary phyletic division of the Acarina should be on that basis.

Thelytoky appears to have developed many times and in species of diverse acarine groups. Its incidence probably has no relationship to the more general and basic method of amphimixis, whether that be haploid arrhenotoky or zygogenesis. As for the method of sex determination, the XY shown by Oppermann for *Argas* is the only convincing case. Other investigators seem not to have been interested in this problem, except Sokoloff, who fails to find sex chromosomes in the Parasitidae (Gamasidae).

General comparisons

Male haploidy as a mode of amphimixis appears to have arisen in different groups of Metazoa from the more usual zygogenetic mode, in which males as well as females are normally diploid and biparental. If we except the very aberrant beetle *Micromalthus*, there is no evidence at present available to show that this change has occurred independently more than five or six times. One of these took place in an ancestral rotifer and may now involve the entire phylum Trochelminthes. Possibly it was a single ancestral mite that gave rise to a stem with many arrhenotokous branches, while another conservatively retained zygogenesis. Whether male haploidy has arisen independently more than once in the Acarina is left for future experiments and observations to decide. Evidence is as yet weak, but there appears to be nothing to prove the existence of a zygogenetic thrips, so that we may imagine a single ancestor of the whole order Thysanoptera as having departed from the mode of his now unknown relatives. The same applies to the Hymenoptera, but here we may speak more positively, in view of the wide scatter and considerable amount of breeding data and cytological study devoted to the order.

Of the two homopteran families showing male haploidy, the aleurodids have no known zygogenetic species. Among the coccids, on the other hand, of the seven subfamilies only the Monophlebinae include known arrhenotokous species. These make up the tribe Iceryini but are absent from the Llaveiini, which are all diploid, and the males of which have XO chromosomes. According to one theory, the aleurodids have been derived from the coccids. They may have descended along with the iceryines from some common ancestor which adopted male haploidy.

This would total but five known independent phyletic arrhenotokous pedigress, with *Micromalthus* as a lone and inconspicuous sixth. Doubtless, other instances may be found, but the ratio with respect to constant thelytoky is likely to remain very low, for new examples of the latter are frequently appearing in the literature.

The change to haploid arrhenotoky has evidently occurred very rarely and has come to involve large taxonomic groups as a stable mode of reproduction. Whether male haploidy may ever revert to zygogenesis is not known. As a test for this possibility, search for normally diploid males should be made in arrhenotokous groups.

The change to thelytoky has occurred and is occurring a great many times in nature, and involves only single scattered species or races. Their adoption of this mode is probably relatively recent, as evidenced by their isolation and by the occurrence of spanandric males among them. Constant thelytoky involves the denial of the advantages of amphimixis and no large or successful group has evolved with this handicap. Only by heterogony, the alternation of a bisexual with one or more parthenogenetic generations, can thelytoky be widely incorporated as a permanent mode of life. Thus thelytoky may be alternated with haploid arrhenotoky, as in the rotifers and the gall-wasps; and thus thelytoky, and in this case also diploid arrhenotoky, may be alternated with a zygogenetic bisexual generation, as in aphids, phyloxerans, and cladocerans. In these three groups a generation of impaternate diploid males and females alternates with one or more generations of agamic females.

Race-hybrid Hypothesis

Tychothelytoky in groups of the XY-male type or tychodeuterotoky in groups of the WZ-female type may be regarded as the most primitive form of natural parthenogenesis. It appears merely as a breakdown of the block to post-meiotic mitosis which has been established in animals but which is absent from plants. Being haploid in origin, it encounters the hazards both of low chromatin content and of recessive lethals, and must undergo both quantitative regulation and stringent selection, respectively.

Parthenogenetic (female) races and species have probably originated from tychothelytoky (1) by oogonial tetraploidy, (2) by advancing cleavage into meiosis so that an oocyte nucleus becomes a cleavage nucleus, (3) by parthenogamy from a polar nucleus, (4) by endomitosis following reduction, or (5) by parthenogamy of cleavage nuclei. The first three of these alternatives involve diploid parthenogenesis with zygosis of the impaternate offspring. The last two involve haploid parthenogenesis with production of a diploid azygote. Chromatin rearrangements, genic mutations, and frequently polyploidy may produce such changes that crossing with the bisexual form becomes ineffective. Sterility and other deviations of the spanandric males from their ancestral type are probably due to these cytogenetic shifts, which modify the original genic balance of the sex chromosome in relation to the autosomes.

At first thought, it may seem that tychoarrhenotoky should logically furnish a first step toward constant arrhenotoky, just as tychothelytoky appears to be the first step toward constant thelytoky. It might be expected that tychoarrhenotoky should occur in groups with WZ-females, if lack of Z should prove lethal. Possibly such a condition may be found among the primitive Lepidoptera or among the related Trichoptera, if these have not acquired by duplication an "autosomal" Z which could render WW females viable. These insect orders, however, constituting a very large and flourishing WZ-female tree, have given rise to no known arrhenotokous branches. If haploid males have various modifications of the factor Z, male haploidy should arise from WZ-female stock rather than from XY-male stock. As regards the mites, coccids, and *Micromalthus*, the cases in which close zygogenetic relatives of the arrhenotokous branches are known, these relatives are of the XY-male type. The suggestion that male haploidy involves female digamety and is thus related to the WZ-female type also meets with the difficulty that through protection of W by Z there has come about a degeneration of the former, so that "backcrossing" becomes fixed as long as WZ functions as the sex differentiator.

The origin of male haploidy through tychoparthenogenesis appears improbable, because few offspring are produced, and these must cross with the zygogenetic stock, thus dispersing the parthenogenetic tendency. A theory involving repeated and extensive race hybridization seems more probable, as furnishing abundant material for natural selection.

Probably modifications within the X-chromosome or within some autosome have occurred, to produce a multiple allelic series and the complementary type of sex determination associated with haploid males. The spanandric males of geographic thelytoky presumably have chromosomes that have undergone modification during their period of protection in the parthenogenetic stock. However, the infrequency and predominant sterility of such males would render infinitesimal the chance of success for any of their few progeny surviving the stringent selection leading toward the goal.

What is needed for the evolution of male haploidy is a large population with a strong tendency toward parthenogenesis and with modified chromosomes and normal chromosomes freely recombining and crossing over and thus originating new types. Such a population might be found in the borderlands between the ranges of an ancestral zygogenetic species and of its thelytokous offshoot. To be specific, let us imagine some ancestral hymenopteran species, some protosiricid of the Early Jurassic for example, in which the zygogenetic stock has already given rise by tychothelytoky to a parthenogenetic (female) scion. The latter, breeding in an isolated territory, has multiplied over a period long enough to accumulate several genetic modifications, but still brief enough for retention of crossability with the parental stock. Now, with increasing population, the areas of stock and scion come to overlap and crossing occurs, at first between the males of the zygogenetic stock and the parthenogenetic females, then between the former and the hybrid females, and later between the members of the segregating fraternities. Thus there is furnished abundant opportunity for cytogenetic recombinations. In this population we might expect great numbers of inviable types to be produced and, among the small proportion of viables, there should be many sterile intersexes. Arrays of genetic types would vary from those needing syngamy to initiate cleavage, at one extreme, to parthenogenetic forms at the other, and from femaleness to maleness.

The viable fertile types should be stabilized at three modes, (1) zygogenesis of both sexes, (2) parthenogenesis of females with males eliminated, (3) zygogenesis of females, parthenogenesis of males. Theoretically, fertile hermaphroditism might be a fourth mode, but this has not been found as a primitive condition in any of the groups which we are considering. Modes (1) and (2) would be reversionary. Mode (3) would furnish the basic material from which the stable arrhenotokous type might evolve. This third type would be produced from combinations in which factors for maleness were recessive, and genes determining parthenogenesis were present. Thus the zygotes would tend to include the females, while the azygotes would be male.

With multiple factors for sex segregating independently, there would be considerable reproductive wastage because of sterile intersexuality. This would tend, by selection, toward a concentration of the effective sex genes into a single closely linked group.

Regulative somatic diploidism of the impaternate males might, for a time, permit normal (diploid) meiosis in spermatogenesis, but since the azygotic embryos would originate as haploids, there should be gradual selection for an increase in chromosome size as a regulative process. This should tend to retard numerical regulation so that, eventually, the entire embryo might become haploid. Since tissues of the germ track are relatively undifferentiated, the spermatogonia especially should retain the initial haploidy of the embryo. The spermatocytes, furnished with the haploid set of chromosomes, would then be faced with the necessity of modifying their type of division, and these modifications should be perfected and standardized by selection.

Genes for enlarged cell size should tend to be concentrated along with the genes for maleness and, like them, should be recessive. Thus the haploid males should come to have cells approximating in size the cells of the females, but the diploid males should have much larger cells, for, to the homozygous recessive genes, there should be added the double amount of chromatin. Diploid males should then be reduced in viability. In *Habrobracon*, it is known that the cell size of diploid males is abnormally large, and there is some evidence that among diploid males larger cell size is associated with higher mortality.

As reduction in spermatocyte meiosis initiated by selection in the haploid males becomes characteristic of the species, the diploid males might also be rendered sterile, as they are in *Habrobracon*. Fixation of the meiotic condition adapted to haploid males should effectively eliminate the few surviving diploid males from reproduction.

Evolution of the sex differentiating segment, called the *x* factor in *Habrobracon*, must have come about by reduction in crossing-over within it and by mutation and the selection of minor factors, so that the various alleles, *xa*, *xb*, *xc*, etc., should come to produce a similar phenotype. Genes governing secondary, as well as primary, sex differences must lie in this chromosome segment, the genes for male traits acting as recessives.

Additional alleles in the series might be brought about as follows: a new allele might originate as some repeat of a local duplication, which would at first give a phenotype somewhat different from the preceding, but this should later be perfected by minor mutations and selection. Whatever disadvantage a new allele might have, because of its production of a divergent phenotype, would tend to be compensated by a selective advantage gained by increasing the number of alleles in the population. Thus in a three-allele population, with the older perfected alleles, *xa* and *xb*, relatively more numerous, these alleles are at a disadvantage because half of the fertilized eggs are wasted (inviable or diploid males), but the matings involving the third allele, *xc*, are much more fecund, even if it be supposed that the females *xa/xc* and *xb/xc* and the males *xc* are somewhat divergent or defective.

In species that are highly differentiated sexually, there may obtain much genetic diversity which does not express itself phenotypically. In this, also, genotypic sex divergence may be greater than genotypic sex convergence without becoming evident. In other words, intersexuality is more obvious than supersexuality, as has been demonstrated in many Lepidoptera, *Lymantria* for example. Seiler's WW females, also, are not only viable but apparently non-separable phenotypically from WZ females. Doubling the genotypic divergence from males, ZZ, produces no visible difference.

It is of interest to note that in all the groups characterized by haploid arrhenotoky, there is a very high degree of sex disparity. The gonadic hermaphroditism of the coccid *Icerya purchasi* appears to be, not a step toward intersexuality, and certainly not in any way primitive, but a secondary modification of a highly differentiated female type, enabling the species to maintain itself and, at the same time, dispense with its highly differentiated males. The sex alleles in haploid arrhenotoky may then differ genically to a considerable extent among themselves without producing perceptible differences. This should aid both in the inception of male haploidy and in the evolution of new alleles in arrhenotokous species.

No phenotypic differences caused by the different sex alleles of *Habrobracon* have yet been demonstrated with certainty. In one inbred stock the males had more antennal segments and the females fewer than in another inbred stock (Whiting, 1943). This indicates the association of genic differences governing antennal segments with the *x*-factor. The apparent unidirectional feminization in gynandroid mosaic males suggests a difference in autonomy of similar structures determined by different alleles.

It is suggested that the various steps outlined above may have brought about the stable condition of amphimixis known as haploid arrhenotoky, not only in the Hymenoptera, but also, at an earlier or later period, in the evolution of the other five or six groups mentioned.

SUMMARY

Among invertebrate animals belonging to seven different groups, a mode of reproduction has been established in which males are haploid, developing parthenogenetically from reduced unfertilized eggs. Five problems involved in the attainment of male haploidy are considered.

(1) Induction of parthenogenetic development in eggs is regarded merely as a breakdown of the block to post-meiotic mitosis which is normally established in animals but is absent from plants.

(2) Viability of the azygote resulting from this initial parthenogenesis is attained by a regulative doubling of chromosome number that corrects the nucleoplasmic ratio, and by selection against recessive lethal factors. The few surviving azygotes are diploid with normally diploid meiosis. Because of their infrequent and scattered occurrence their production has been called tychoparthenogenesis.

(3) Meiosis in the haploid male has been modified in different ways in different groups. This has come about by a selective process when the spermatocytes have received a haploid set of chromosomes.

(4) Sex determination in these groups is regarded as complementary, depending upon a single series of multiple alleles having similar effects phenotypically. Each allele is considered a chromosome segment containing many genes, dominant female-producing and recessive male-producing. Females are heterozygous, normal haploid males are recessive. The homozygous recessive combinations (infrequent because of multiple allelism) are inviable or may occasionally develop as diploid males.

(5) Haploidy of the azygous males may be defined as having the haploid type of spermatogenesis, with chromosome reduction lacking. Somatically, these males may be haploid, at least in early developmental stages, or they may have secondary diploidy or polyploidy, as in the drone of

the honey bee, which begins as a diploid because of precocious splitting of the ootid monads.

The hypothesis of the gradual degeneration of one set of chromosomes in the attainment of haploid male viability and in the regulation of meiosis, advanced by Schrader and Hughes-Schrader (1931) on the basis of their studies of coccids, is questioned. It is considered that their postulated stages in chromosome degeneration (asynapsis, heteropycnosis, and male haploidy) are independent phenomena.

Male haploidy is apparently characteristic of the entire insect order Hymenoptera, and probably of thrips and rotifers. A single beetle, *Micromalthus*, has haploid males. It is suggested that the primary phyletic division of the mites, Acarina, may be made on this basis. Among the coccids, the tribe Iceryini are characterized by male haploidy, and it is possible that the related homopteran family Aleurodidae may be derived in common with this tribe.

According to Vandel (1936) parthenogenetic (female) races and species have originated from tychoparthenogenesis by extension of the process of chromosome doubling into meiosis, so that the type of parthenogenesis becomes diploid from the beginning, and a fixed mode of reproduction. Further doubling lies at the basis of the polyploidy characteristic of many parthenogenetic races.

A review and discussion is given of some of the recently published cases of tychoparthenogenesis and of the fixed parthenogenesis of unisexual (female) races and species.

As a possible explanation of the origin of male haploidy, an hypothesis is suggested of hybridization between a normal bisexual race and a parthenogenetic (female) race in which the chromosomes have become modified. Among the segregating types resulting from this hybridization there should be azygous males. Nucleoplasmic regulation in these males should be gradually modified by an increase in the size of chromosomes, so that the haploid number might be retained into progressively later embryonic stages, especially in the germ track. In this way meiosis of the spermatocytes should be changed from the diploid to the haploid type.

LIST OF LITERATURE

André, M. 1935. La parthénogenèse chez les acariens. *Ann. Sci nat. Zool*, 18: 103–118.

Astaurov, B. L. 1940. Artificial parthenogenesis in the silk-worm (*Bombyx mori* L.). *Izdatel'stvo Akad. Nauk USSR*, Moscow, 240 p.

Badonnel, A. 1938. Sur la biologie de *Psyllipsocus ramburi* S. L. (Psocoptera). *Bull. Soc Ent. France*, 43: 153–158.

Beadle, G. W. 1930. Genetical and cytological studies of mendelian asynapsis in *Zea mays*. Paper #172, Dept. Plant Breeding, Cornell Univ., Ithaca.

Bleier, H. 1933. Die Meiosis von Haplodiplonten. *Genetica*, 15: 129–176.

Bridges, C. B. 1925. Sex in relation to chromosomes and genes. *Amer. Nat.*, 59: 127–137.

——. 1930. Haploid *Drosophila* and the theory of genic balance. *Science*, 72: 405–406.

Brues, C. T. 1928. A note on the genus *Pelecinus*. *Psyche*, 35: 205–209.

Cappe de Baillon, P. 1939. Sur la parthénogenèse des Tettigonidae (Orthopteres). *C. R. Acad. Sci. Paris*, 208: 463–465.

——, and de Vichet, G. 1939. La cytologie des males et l'hypothese du rajeunissement periodique de la race par la fécundation chez les Phasmes à parthénogenèse constante. *C. R. Acad. Sci. Paris*, 209: 525–527.

——, and ——. 1940. La parthénogenèse des espèces du genre *Leptynia* Pant (Orthopt. Phasmidae). *Bull. biol. Paris*, 74· 43–87.

Cooper, K. W. 1937. Reproductive behavior and haploid parthenogenesis in the grass mite, *Pediculopsis graminum* (Reut.) (Acarina, Tarsonemidae). *Proc. Nat. Acad. Sci. Wash.*, 23: 41–44.

——. 1939. The nuclear cytology of the grass mite, *Pediculopsis graminum* (Reut.) with special reference to karyomerokinesis. *Chromosoma*, 1·51–103.

Creighton, M. 1938. Parthenogenesis in *Chorthippus curtipennis*. *Genetics*, 23: 145.

Davidson, J., and Bald, J. G. 1931. Sex determination in *Frankliniella insularis* Franklin (Thysanoptera). *Austral. J. exp. Biol. med. Sci.*, 8: 139–142.

Dodds, K. S. 1938. Chromosome numbers and spermatogenesis in some species of the hymenopterous family Cynipidae. *Genetica*, 20: 67–84.

Doncaster, L. 1916. Gametogenesis and sex determination in the gall-fly, *Neuroterus lenticularis*. Part III. *Proc. Roy. Soc. B.*, 89: 183–200.

Dozorceva, R. L. 1936a. Chromosome morphology in *Pteromalus puparum*. *Bull. (Isvestia) Acad. Sci. URSS, Ser. Biol.*, 1209–1221.

——. 1936b. On determination of sex in *Pteromalus puparum*. *Bull. (Isvestia) Acad. Sci., URSS, Ser. Biol.*, 1223–1233.

——. 1936c. Sex-linked heredity in *Pteromalus puparum*. *C. R. (Doklady) Acad. Sci. URSS*, 3: 335–338.

——. 1936d. The morphology of chromosomes in the ichneumon *Pteromalus puparum*. *C. R. (Doklady) Acad. Sci., URSS*, 3: 339–342.

Dreyfus, A., and Breuer, M. E. 1944. Chromosomes and sex determination in the parasitic hymenopteron *Telenomus fariai* (Lima). *Genetics*, 29: 75–82.

Dzierzon, J. 1845. *Eichstädte Bienenzeitung*, 1: 113.

Ewing, H. E. 1934. The suborders and superfamilies of Acarina *Proc. Helminth. Soc. Wash.*, 1: 64–65.

Fankhauser, G. 1938. Sex differentiation in a haploid salamander, *Triton taeniatus* Laur. *Jour. exp. Zool.*, 79: 35–49

Goldschmidt, R. 1917. On a case of facultative parthenogenesis in the gypsy-moth *Lymantria dispar* L. with a discussion of the relation of parthenogenesis to sex *Biol. Bull*, *32* . 35–43.

Greenshields, F. 1936a Chromosomal relationship between males and females in Hymenoptera Symphyta. *Nature, Lond*, 137: 662, 746

——. 1936b. Tetraploidy and Hymenoptera. *Nature, Lond.*, 138: 330.

Hughes-Schrader, S. 1927. Origin and differentiation of the male and female germ cells in the hermaphrodite of *Icerya purchasi* (Coccidae). *Z. Zellforsch.*, 6: 509–540.

——. 1930. The cytology of several species of iceryine coccids with special reference to parthenogenesis and haploidy. *Jour. Morph. Physiol.*, 50: 475–495.

——. 1935. The chromosome cycle of *Phenococcus* (Coccidae). *Biol. Bull.*, 69· 462–468.

Illgen, H. 1914. Zur Kenntnis der Spermatogenese und Biologie bei *Seison grubei* Claus. *Zool. Anz.*, 44: 550.

Inaba, F. 1939. Diploid males and triploid females of the parasitic wasp *Habrobracon pectinophorae* Watanabe *Cytologia*, 9: 517–523.

Kawamura, T. 1939. Artificial parthenogenesis in the frog. II. The sex of parthenogenetic frogs. *J. Sci. Hirosima Univ.* B (Div. 1), 7: 39–86.

King, R. L., and Slifer, E. H. 1933. Genetic analysis of parthenogenesis in Nabours' grouse locusts. *Amer. Nat*, 67: 80–81.

——, and ——. 1934. Insect development VIII. Maturation and early development of unfertilized grasshopper eggs. *J. Morph.*, 56: 607–619.

Light, S. F. 1944. Parthenogenesis in termites of the genus *Zootermopsis*. *Univ. Calif. Pub. Zool.*, 43: 405–412.

Matthey, R. 1941. Etude biologique et cytologique de *Sago pedo* Pallas (Orthoptères-Tettigonidae). *Rev. Suisse Zool.*, 48: 91–141.

Metz, C. W. 1938. Chromosome behavior, inheritance and sex determination in *Sciara*. *Amer. Nat.*, 72: 485–520.

Miller, H. M. 1931. Alternation of generations in the rotifer *Lecane inermis* Bryce. *Biol. Bull.*, 60: 345–381.

Milliron, H. E. 1939. A parthenogenetic new species of the genus *Perimegatoma* Horn (Coleoptera; Dermestidae). *Ann. Ent. Soc. Amer.*, 32: 570–574.

Morrill, A. W., and Back, E. A. 1911. White flies injurious to citrus in Florida. *U. S. Dept. Agri., Bur. Ent. Bull.*, 92: 57–94.

Muller, H. J. 1918. Genetic variability, twin hybrids and constant hybrids, in a case of balanced lethal factors. *Genetics*, 3: 422–499.

Nabours, R. K. 1929. *The genetics of the Tettigidae.* The Hague: Martinus Nijhoff.

——. 1930. Induced parthenogenesis and homozygosis. *Science*, 72. 502–503.

Nachtsheim, H. 1913. Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (*Apis mellifica* L.) *Arch. Zellforsch*, 11: 169–241.

Oehninger, M 1913. Über Kerngrossen bei Bienen. *Verh. phys.-med. Ges. Wurzburg* (n F.), 42: 135–140.

Ohmachi, F 1929 Preliminary note on a case of facultative parthenogenesis in *Loxoblemmus frontalis* Shir. (Gryllidae). *Proc. Imp. Acad. Tokyo*, 5· 367–369.

Oppermann, E. 1935. Die Entstehung der Riesenspermien von *Argas columbarum* (Shaw) (reflexus F.). *Z. mikr. anat Forsch*, 37: 538–560.

Parmenter, C. L. 1940. Chromosome numbers in *Rana fusca* parthenogenetically developed from eggs with known polar body and cleavage histories. *J. Morph*, 66: 241–260.

Pätau, K. 1934. Ein neuer Fall haploider Parthenogenese. *Naturwiss.*, 22: 648–649.

——. 1936 Cytologische Untersuchungen an der haploid-parthenogenetischen Milbe *Pediculoides ventricosius*. (Newp.). *Berl. Zool. Jb.*, 56. 277–322.

Patterson, J. T. 1928a. Sexes in the Cynipidae and male-producing and female-producing lines. *Biol. Bull.*, 54: 201–211.

——. 1928b. Functionless males in two species of *Neuroterus*. *Biol Bull.*, 54: 196–200.

——, and Hamlett, G. W. D. 1925. Haploid males in *Paracopidosomopsis*. *Science*, 61: 89.

Peacock, A. D., and Gresson, R. A. R. 1931. Male haploidy and female diploidy in *Sirex cyaneus* F. (Hymen.). *Proc. Roy. Soc. Edinb.*, 51.

Pincus, G., and Shapiro, H. 1940. The comparative behavior of mammalian eggs *in vivo* and *in vitro*. VII. Further studies on the activation of rabbit eggs. *Proc. Amer. Philos. Soc.*, 83: 631–647.

Putnam, W. L. 1939. The plum nursery mite (*Phyllocoptes fockeui* Nal. and Trt.). *Ann. Rept. Ent. Soc. Ontario*, 70: 33–39.

Robertson, W. R. B. 1930. Chromosome studies V. Diploidy and persistent chromosome relations in parthenogenetic Tettigidae. *J. Morph. Physiol.*, 50: 209–258.

Ross, E. S. 1940. A revision of the Embioptera of North America. *Ann Ent. Soc. Amer.*, 33: 629–676.

Sanderson, A. R. 1932 The cytology of parthenogenesis in Tenthredinidae. *Genetica*, 14: 321–493.

Schmieder, R. G. 1938. The sex ratio in *Melittobia chalybii* Ashmead, gametogenesis and cleavage in females and in haploid males (Hymenoptera: Chalcidoidea). *Biol. Bull*, 74: 256–266.

Schrader, F. 1920. Sex determination in the white fly (*Trialeurodes vaporariorum*). *J. Morph.*, 34: 267–305.

—— 1923. Haploidie bei einer Spinnmilbe. *Arch. mikr. Anat*, 97: 610–622

——. 1926. Notes on the English and American races of the greenhouse white fly (*Trialeurodes vaporariorum*) *Ann. appl. Biol.*, 13.

——, and Hughes-Schrader, S 1926 Haploidy in *Icerya purchasi*. *Z. wiss. Zool*, 128. 182–200.

——, and ——. 1931. Haploidy in Metazoa. *Quart. Rev. Biol.*, 6: 411–438.

Scott, A. 1936. Haploidy and aberrant spermatogenesis in a coleopteran, *Micromalthus debilis* LeConte. *J. Morph.* 59. 485–515

——. 1938 Paedogenesis in the Coleoptera. *Z. Morph. Ökol Tiere*, 33: 633–653

——. 1941 Reversal of sex production in *Micromalthus*. *Biol. Bull*, 81: 420–431.

Seiler, J. 1923 Geschlechtschromosomen-Untersuchungen an Psychiden. *Z. ind. Abst- Vererb.*, 31: 1–99.

——, and Schaeffer, K. 1941. Der Chromosomenzyklus einer diploidparthenogenetischen *Solenobia triquetrella* Die automiktischen Vorgänge zu Beginn der Furchung *Rev. Suisse Zool.*, 48: 537–540.

Shull, A. F. 1917 Sex determination in *Anthothrips verbasci*. *Genetics*, 2: 480–488.

——. 1929. Determination of types of individuals in aphids, rotifers and *Cladocera*. *Biol. Rev.*, 4: 218–248.

Slifer, E. H., and King, R. L. 1932. Parthenogenesis and haploidy in grasshoppers (Acrididae). *Proc. 6th Intern. Cong. Genetics*, 2: 187.

Smith, S. G. 1941. A new form of spruce sawfly identified by means of its cytology and parthenogenesis. *Sci. Agric.* (Ottawa), 21: 245–305.

Smith, T. L. 1938. Genetical studies in the wax moth *Galleria mellonella* Linn. *Genetics*, 23: 115–137.

Sokoloff, I. 1934. Untersuchungen über die Spermatogenese bei den Arachniden. V. Über die Spermatogenese der Parasitidae (= Gamasidae, Acari). *Z. Zellforsch.*, 21: 42–109.

Speicher, B. R. 1935. Cell size and chromosomal types in *Habrobracon*. *Amer. Nat.*, 69: 79–80.

——. 1936. Are Hymenoptera tetraploid? *Nature, Lond.*, 138: 78.

——. 1937 Oogenesis in a thelytokous wasp, *Nemeritis canescens* (Grav.). *J. Morph.*, 61: 453–471.

Speicher, B R., and Speicher, K. G. 1940. The occurrence of diploid males in *Habrobracon brevicornis*. *Amer. Nat.*, 74. 379–382

Speicher, K. G. 1934. Impatemate females in *Habrobracon*. *Biol. Bull*, 67: 277–293.

Speicher, K. G, and Speicher, B R. 1938. Diploids from unfertilized eggs in *Habrobracon*. *Biol. Bull.*, 74: 247–252.

Stoll, N. R., and Shull, A. F. 1919. Sex determination in the white fly. *Genetics*, 4: 251–260.

Sturtevant, A. H. 1923. The probable occurrence of parthenogenesis in *Ochthiphila polystigma* (Diptera). *Psyche*, 30: 22–27.

Suomalainen, E. 1940. Polyploidy in parthenogenetic Curculionidae. *Hereditas*, 26: 51–64.

Székessy, W. 1937 Über Parthenogenese bei Koleopteren. *Biolog. Gen.*, 12 577–590.

Tauson, A. 1927. Die Spermatogenese bei *Asplanchna intermedia* Huds. *Z. Zellforsch.*, 4: 652–681.

Thienemann, A., and Strenzke, K. 1940a. Terrestrische Chironomiden. III–IV. Zwei parthenogenetische Formen. *Zool. Anz.*, 132: 24–40.

——, and ——. 1940b. Terrestrische Chironomiden. VI. *Pseudosmittia holsata*, eine neue Art mit fakultativen Parthenogenese. *Zool. Anz.*, 132: 238–244.

Thomsen, M. 1927. Studien über die Parthenogenese bei einigen Cocciden und Aleurodiden. *Z. Zellforsch*, 5. 1–116.

——. 1929. Sex determination in *Lecanium*. Trans. IV. *Intern. Cong. Entomol. Ithaca* (1928), 1: 18–24.

Torvik-Greb, M. 1935. The chromosomes of *Habrobracon*. *Biol. Bull*, 68: 25–34.

Tuzet, O., and Millot, J. 1937. Récherches sur la spermiogenèse des Ixodes. *Bull. Biol. France Belg.*, 71: 190–205.

Vandel, A. 1931a. *La Parthénogenèse* Paris: Encyclopédie Scientifique

——. 1936. L'evolution de la parthénogenèse naturelle. *C. R. XII Cong. Intern. Zool. Lisbonne (1935)*, 1: 51–64

——. 1937. Chromosome number, polyploidy and sex in the animal kingdom. *Proc. Zool. Soc. Lond., Ser. A.*, 107: 519–541.

——. 1938. Recherches sur la sexualité des Isopodes. III. Le déterminisme du sexe et de la monogénie chez *Trichoniscus* (*Spiloniscus*) *provisorius* Racovitza. *Bull. Biol. France Belg.*, 72: 148–186.

——. 1940. La parthénogenèse géographique. IV. Polyploïdie et distribution geographique. *Bull. Biol. France Belg.*, 74: 94–100.

Warmke, H. E., and Blakeslee, A. F. 1940. Further differences in the determination of sex in *Melandrium* and *Drosophila*. *Collecting Net*, 15: 174.

Wesenberg-Lund, C. 1923. Contributions to the biology of the Rotifera. *Mem. Acad. Roy. Sci. Lettres Danemark, Copenhague, Sect. Sci.* (8) 4: 189.

——. 1930. II. The periodicity and sexual periods. *Mem. Acad. Roy. Sci. Lettres Danemark, Copenhague, Sect. Sci.*, (9) 2: 3.

Whiting, P. W. 1935. Sex determination in bees and wasps. *J. Hered.*, 26: 263–278.

——. 1940a. Multiple alleles in sex determination of *Habrobracon*. *J. Morph.*, 66: 323–355.

——. 1940b. Sex-linkage in *Pteromalus*. *Amer. Nat.*, 74: 377–379.

——. 1943. Multiple alleles in complementary sex determination of *Habrobracon*. *Genetics* 28: 365–382.

——, Greb, R. J., and Speicher, B. R. 1934. A new type of sex-intergrade. *Biol. Bull.*, 66: 152–165.

——, and Speicher, K. G. 1935. Impaternate daughters of females heterozygous for a sex-linked gene in *Habrobracon*. *Amer. Nat.*, 69: 82–83.

——, and Whiting, A. R. 1927. Gynandromorphs and other irregular types in *Habrobracon*. *Biol. Bull.*, 52: 89–121.

Whitney, D. D. 1929. The chromosome cycle in the rotifer *Asplanchna amphora*. *J. Morph. and Physiol.*, 47: 417.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

EVOLUTION: A SYNTHESIS OF GENETICS AND PALEONTOLOGY.

Being a review of *Tempo and Mode in Evolution*, by *George Gaylord Simpson*. New York (Columbia Biological Series Number XV, Columbia University Press). $3.50. xviii + 237 pp. 1944.

By Bentley Glass, Goucher College

The study of the causes and mechanisms of evolution has in the past decade received a fresh and profound impetus through the application, on the one hand, of the statistical theories developed chiefly by Fisher, Haldane, and Wright, and on the other, through the application of experimental methods to the study of evolutionary changes. The publication of Dobzhansky's *Genetics and the Origin of Species* in 1937 marks the beginning of this new era in many minds, for that book first unified the new concepts and presented a stimulating and well-ordered survey of evolutionary change on three levels, those of the raw material—gene and chromosome mutations; the action of natural selection and other factors determining the fixation or loss of genes in populations; and the influence of isolation, geographical and genetic, in perpetuating population differences and establishing species. The widening influence of this book and of the mathematical theories of evolutionary change has been reflected in recent years in a number of books of outstanding significance. *The New Systematics* (ed., Julian Huxley) and Mayr's *Systematics and the Origin of Species* reveal the invigorating effect of new ideas upon old-style taxonomy, and have blazed new trails for investigators to follow. Darlington, in *The Evolution of Genetic Systems*, has, in brilliant speculations based upon cytological data, outlined aspects of evolution heretofore little considered. Goldschmidt, in *The Material Basis of Evolution*, has developed radical ideas about the origin of species and higher systematic categories. Julian Huxley has assembled and collated an enormous mass of data bearing on the varied modes of speciation in *Evolution: the Modern Synthesis*, and has developed his original ideas of progress in evolution and the significance of dominant forms.

The most recent addition to this group, *Tempo and Mode in Evolution*, is fully worthy of their company and may well be ranked with the best of them. Certainly no scientific book in recent years has kept the present reader so continuously excited that each fresh page seemed an adventure, each new chapter an exploration of a Terra Nuova. There is good reason for this feeling. Between no branches of evolutionary biology has the chasm yawned wider than between paleontology and genetics. The geneticist has been prone to regard the paleontologist as a misguided believer in mystic orthogenesis, whose sole contribution to biology was the long-since demonstrated truth of evolution. The paleontologists, on the other hand, in Simpson's own words, "felt that a geneticist was a person who shut himself in a room, pulled down the shades, watched small flies dissporting themselves in milk bottles, and thought he was studying nature. A pursuit so removed from the realities of life, they said, had no significance for the true biologist." There has been no one competent enough in both fields to bridge the gap between them. Yet there are common problems which are only capable of solution through combined attack. In particular, as Simpson points out, the study of evolutionary rates and patterns requires such an approach. It is these aspects of evolution that Simpson considers under the headings "Tempo" and "Mode."

The treatment is therefore by design a limited one. This is neither a large nor an exhaustive book. Its genius lies, in the first place, in the application of genetic concept to paleontological data; in the second place, to the grasp and originality of Simpson's thought. It is not too much to say that hereafter no treatise on the causes and modes of evolution can ignore it, no paleontological interpretation proceed from previous bases. As a geneticist, the reviewer is filled with admiration of the clear understanding and able exposition of genetic thought manifested by the author to a degree that makes one feel somewhat envious. To a biologist only slightly acquainted with the data of paleontology, on the other hand, the effective, intelligible way in which the author selects and presents the material from his own field is equally admirable.

In an introductory chapter, Simpson deals with rates of evolution—rates absolute and relative, rates in genetically related unit characters and in genetically independent characters, correlative rates, rates of single characters, of entire organisms, and of groups. Illustrations are drawn chiefly from the evolution of the Equidae, establishing the theses that "(1) the rate of evolution of one character may be a function of another character and not genetically separable, even though the rates are not equal; (2) the rate of evolution of any character or combination of characters may change markedly at any time in phyletic evolution, even though the direction of evolution remains the same; (3) the rates of evolution of two or more characters within a single phylum may change independently; (4) two phyla of common ancestry may become differentiated by differences in rate of evolution of different characters, without marked qualitative differences or differences in direction of evolution." Rates correlated with an external factor (thickness of strata) are illustrated from the ammonite *Kosmoceras*. Rates of evolution of entire organisms as units are found to be approximately equal in chalicotheres and horses, while those of ammonites are much slower. Survivorship curves for genera of pelecypods and land carnivores are found to be different, and, for the Carnivora, the number of genera existing at any one time, the rate of origin of new genera, and the rate of disappearance of genera are positively correlated with one another, and presumably with rate of evolution.

The next topic is that of the "Determinants of Evolution." Variability, rate of mutation, character of mutations, length of generations, size of population, and selection are considered with thorough grasp of genetic thought. Simpson's criticism of Goldschmidt's view that "systemic" mutations are of prime importance in the origin of species and higher categories is one of the most cogent that has been offered. His application of the mutation theory to paleontologists' disputes over the continuous or discontinuous origin of new characters is convincing. An unfortunate series of typographical errors should be noted here. On pp. 66–68, in discussing the effects of population size, a number of formulae are written 1/2 N, 1/2 s, 1/4 μ, etc., instead of the correct forms $\frac{1}{2N}, \frac{1}{2s}, \frac{1}{4\mu}$. This may create considerable difficulty in following the argument, for all those not aware of the error.

Simpson next distinguishes between micro-evolution ("changes within potentially continuous populations"), macro-evolution ("rise and divergence of discontinuous groups"; "rise of species and genera"), and mega-evolution ("large-scale evolution studied by the paleontologist"; "differentiation between families, orders, classes, and phyla"). The primary question here is that of the nature of the discontinuities that become more and more common at higher levels. It is shown that minor discontinuities can be referred with probability to stratigraphic hiatuses, or to sampling of migrants instead of main lines. On the other hand, the major discontinuities, as strikingly exemplified in the origins of the mammalian orders, remain to be accounted for. Here the author develops his major original contribution to theory. He proposes that "mega-evolution normally occurs among small populations that become pre-adaptive and evolve continuously (without saltation, but at exceptionally rapid rates) to radically different ecological positions."

The author then passes to the examination of low-rate (bradytelic) and high-rate (tachytelic) lines, developing the thesis that both of these arise from normal-rate (horotelic) lines that vary in normal frequency fashion, so that extreme variant horotelic lines are with difficulty distinguished from the true low-rate and high-rate lines. There are numerous classic examples of low-rate lines. Simpson suggests that these normally have large breeding populations, arise through rapid evolution, are predominantly and closely adaptive in an ecological situation that is only slightly or periodically variable. The high-rate lines, on the other hand, "either become extinct or usher in new major adaptive grades." The significance of relicts is also discussed

In a chapter, "Inertia, Trend, and Momentum," the phenomenon of rectilinear (orthogenetic) evolution is taken up, and again the trends in the Equidae furnish the main evidence. The conclusion reached will satisfy geneticists but probably not all paleontologists: "A dispassionate survey suggests that much of the rectilinearity of evolution is a product rather of the tendency of the minds of scientists to move in straight lines than of a tendency of nature to do so." Of course, Simpson also recognizes the possibility of orthoselection and of secondary trends correlated with a selective trend. Momentum effects he regards as only apparent, interpretable on a variety of genetic bases.

The remainder of the book is hardly more than a sketch of Simpson's theoretical thinking. It contains two chief ideas which are briefly developed. First, animals occupy adaptive zones of the environment, but occupation of a zone depends on the preadaptation of the environment and of the organism, as well as the zone's vacancy or occupancy only by a less well adapted group.

Secondly, there are three main modes of evolution. Speciation takes place within an adaptive zone, from subzone to subzone. Phyletic evolution takes place within one adaptive zone as it slowly changes character. (This resembles Huxley's successional species.) *Quantum evolution* takes place in the step-like shift from one adaptive zone to another, giving rise to distinctly new adaptive types. It may be divided into an inadaptive phase, a preadaptive phase, and a final adaptive phase. It is illustrated by the origin of hypsodonty in horses. Populations in quantum evolution are unstable, small, tachytelic, with a rectilinear mode of change of short duration. The small population and the rapidity of the change account for the hiatus in the fossil record. The concept of quantum evolution Simpson regards as the most important, if also the most controversial and hypothetical one that he has advanced.

Some readers will undoubtedly feel that the supporting evidence for the volume of theory is rather thin. Simpson would probably agree. From intent, the discussion has been kept free of the superfluity of examples which in many books of this sort chokes the flow of thought, obfuscating rather than clarifying the central ideas. Where there is a genuine paucity of evidence, thinking such as this, soundly based on what is known, is the one thing most likely to stimulate the research that will produce evidence, either for or against. No student of evolution, from this day forth, can afford to be ignorant of *Tempo and Mode in Evolution.*

REVIEWS AND BRIEF NOTICES

GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

PROCESS AND POLARITY. *Woodbridge Lectures Number 1, Delivered at Columbia University 1943.*

By Wilmon Henry Sheldon. Columbia University Press, New York. $2.00. xvi + 153 pp. 1944.

This book offers four things of general interest: (1) a theory of truth; (2) a critical analysis of important world-views; (3) an attempt to show that polarity and "process" are pervasive aspects of reality; and (4) side-lights on the general nature of certain things studied by the special sciences.

Sheldon's theory of truth may be boiled down to something like this: just as the good for an animal is whatever adapts it to its environment, so the true for man is whatever in the way of belief brings success. For Sheldon, "success" means survival, the completion of intended acts, and living more fully and intensely. Thus the pathway to truth is empirical, pragmatic, and experimental. To him, theoretical tests of truth, such as inclusiveness and consistency, are of subordinate value, and the common error of the past has been the dependence on theoretical tests chiefly or exclusively.

Of the many "world-maps" which philosophers have produced, he thinks that five have satisfied the practical test of truth and have therefore survived: materialism, idealism, scholasticism, process-philosophy, and irrationalism. But no one of these is sufficient. Sheldon characterizes each and comments on its merits and its defects.

Sheldon's own philosophy might be called a sixth type, since it stresses both polarity and "process" as pervasive characteristics of reality. Things are groups of polars; and polarity is itself in a polar relation to "process." Two things are in a polar relation when they satisfy four conditions; they must be: (1) opposites; (2) balanced; (3) to a degree cooperative; and (4) to a degree independent. Sheldon offers a detailed analysis of only what seem to him the three most fundamental of polar pairs: (1) body-mind; (2) one-many; and (3) structure-process.

Sheldon thinks that the greatest discovery of modern times is "process": the existence of irreversible change in which the old is preserved and an increment of novelty emerges, so that there is a progress toward fullness of being. Change thus becomes "an efficient agent in itself," an eternally creative power, and not merely a phase of substance or a stage in the development of substance, and still less just a replacing of one substance by another. Also time—because it is the essence of change—comes to be regarded, like change, as a positive and ultimate principle. In a lyrical passage on the role of "process," Sheldon writes: "Process is nature's great remedy, the healing potion supplementing the imperfections that mar the polar order, the hope and lure of the future and the basis of a working confidence in progress. It is the office of the process-principle to remove the clash and conflict between the polar opposites, restoring their energy for the free variation they should have unmolested. And this free variation means more novelty, ministering in turn to the phase of process. . . ." Reality, for Sheldon, may be diagrammed as a growing spiral with ever larger circles—a logarithmic spiral whose timeless equation defines its indefinite expansion.

Unlike Bergson, Sheldon finds irreversible change in the inorganic world; e.g., the motions of electrons in a current, and heat radiation. On the level of minute phenomena, natural laws are statistical laws, i.e., laws of probability or chance (in its modern meaning). Nature is imprecise, always deviating from exact law. Elementary possibles occur with equal frequency, and gradually every possible and combination of possibles has its opportunity to exist as the process approaches an even distribution. An emergent factor is obvious.

The differentia of living things, according to Sheldon, are: (1) self-perpetuation, (2) growth, and (3) reproduction. While self-perpetuation represents reversible change, growth is normally irreversible, especially where it involves a hierarchy of levels; and reproduction and the evolution of species are also irreversible. Heredity follows a statistical law which indicates that all possible combinations of genes tend to occur with equal frequency. This means "process" with its incremental variation. Structure and behavior, both ontogenetically and phylogenetically, are in a polar relation to one another, as are also plant life and animal life. He regards the differentia of the mental as: (1) the tendency to look before and after—the ability to recall the past and plan the future; (2) the desire to seek some goods for the future, or aspiration; and (3) a totality, or synthesis, which in some measure determines its details or parts. The progress of knowledge is irreversible, both in the person and in the accumulation of race experience. Knowledge-seeking and end-seeking are polar opposites.

Sheldon's study should probably be read primarily for its suggestiveness. Readers who are looking for consistency, clear cut definition and incontrovertible argument will be disappointed. Indeed, Sheldon goes out of his way to castigate those whose first concern is precision and non-contradiction. "Better an ounce of significance than a pound of precision" is his motto. This is part of an irrationalism which shows itself at times in his pages and which includes also: (1) a subordination of the rational criteria of truth to the practical criterion of "success"—with an occasional acceptance of "direct insight"; (2) a depreciation of "thought"; (3) a denial of the ability of science to "account for" anything; (4) the attribution of philosophical preferences to non-rational factors; (5) a tendency to equate the essence of the real, true, and good with sheer power (the reservations inserted to avoid being driven from this position to an approval of egoism, power politics, etc., being left undefended). An important consequence (or cause) of this irrationalism is that Sheldon overlooks the rational aspects of the experimental method in its most reliable form. For example, it is not the getting of intended results or of desirable practical consequences (whether intended or not) which constitutes the most dependable test of truth. It is rather the observing of what one had a *rational* right to expect to be able to observe, on the assumption that the hypothesis which guided experimental procedure is true. The *intellectual* noting of the correspondence between the *logically* reached prediction and the later observation, is what proves the hypothesis true; not the correspondence of the practical consequences with what was wanted or willed.

RAYMOND P. HAWES

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SCIENCE AND THE IDEA OF GOD.
By William Ernest Hocking. The University of North Carolina Press, Chapel Hill, North Carolina. $1.50. ix + 124 pp. 1944.

FROM SCIENCE TO GOD.
By Karl Schmidt. Harper and Brothers. $2.00. x + 169 pp. 1944.

In recent years there has been held on the Atlantic seaboard an annual conference on science, philosophy, and religion. The reports of these conferences are generally out of print a few days after they are put on sale, a fact which indicates the widespread interest in the conferences on the part of the general public.

A generation ago any attempt to unify these three fields would have been called a reconciliation. Today the word used is integration, and the difference in meaning between these terms is an excellent index to the difference in attitude between nineteenth and twentieth century minds. A reconciliation involves a certain amount of concession and adjustment, based upon a mutual give and take. In the nineteenth century there were three outstanding reconcilers, one in each field—Le Conte in science, Fiske in philosophy, and Drummond in religion. All of these built on the foundation of Darwinian evolution, which from its origin in a specific field of biology has permeated all fields of thought and has had a unifying influence unparalleled in the history of human intelligence.

Today this synthesis has ceased to be a reconciliation, but it has not yet become an integration. We still tend to try to confine our scientific, philosophic, and religious beliefs in hermetically insulated compartments of our minds—an achievement possible only because we are all partly schizophrenic. It is interesting to speculate as to whether the present sorry state of civilization may not be due to the ubiquity of schizophrenia among those who determine international policies.

For such reasons as these any attempt to establish an integrated mind at the present time is not only appropriate but indeed most welcome. Schmidt's book, although small in bulk, is an ambitious attempt to establish theology on scientific basis. His argument is very ingenious, and runs somewhat as follows:

Your thoughts are not my thoughts, neither can I remember your experiences nor can you remember mine. The thoughts that bring you happiness may bring me sorrow, and vice versa. Your emotional responses may be very different from mine to the same stimulus. The only conclusion that we can draw from this is that your mind and my mind are distinct entities. And yet, you and I agree in our judgments in far too many instances for us to attribute the agreement to random coincidence. Without such agreement no science would be possible. Emmanuel Kant accounted for this agreement by postulating his *Ding an sich* and saying that when different minds contemplate the same object, they must necessarily come to the same conclusion. But since all of our knowledge of external objects comes through the senses, this is equivalent to defining that of which we have experience in terms of that of which we have no experience, which is no explanation at all. The only alternative is that there must be an Omniscient Intelligence who thinks these thoughts through our finite minds.

There are two implications contingent upon such an assumption. Since it is inconceivable that such an Omniscient Intelligence could think an untruth, the criterion of the truth of a belief is the universality with which it is held. If it be true that the majority is always wrong at first, it is also true that eventually the truth will always prevail.

The other implication is that a universe without such an Omniscient Intelligence would be a chaotic universe. There could be no agreement among different minds, no common interpretation of external phenomena, no formulation of natural law, and therefore no science.

This implication is strangely inconsistent with the author's criticism of Isaac Newton, who postulated a first cause to start the universe going. The author states that there would then be no further need of such a Supreme Intelligence, inasmuch as natural law would suffice to keep the universe in motion. As a matter of fact, however, natural law is not a prime mover but a descriptive formula, and the fact that the processes of nature can be described by a formulated law is the best possible kind of evidence of the existence of a Supreme Intelligence.

Hocking's series of McNair lectures runs aground on the same reef. In his first lecture, he maintains that a universe so dependable that natural laws can be formulated to describe its past and to forecast its future cannot be ruled by a God who answers prayer. His remaining lectures are devoted to showing that only with such a universe is the existence of such a God compatible. The perusal of his book leaves the reader in a state of mental confusion—not so much as to what the reader should think or can think, but as to what Hocking really does think. Perhaps this was Hocking's object—to make the reader arrive at a conclusion for himself, without giving his own away.

A really scientific treatise on the interrelations of science, philosophy, and religion still remains to be written.

THE ROMANCE OF EXISTENCE.

By Ross Bundy. Pitman Publishing Corporation, New York. $2.00. vii + 188 pp. 1944.

This work is an example of what is technically called 'fine writing." What the author has to say is subordinated to the way in which he says it. Consequently the book must be judged as literature rather than as science. This does not mean that the author's knowledge of science is defective—it means merely that scientific knowledge has been demoted to a position in which it serves chiefly as a display case for the author's fluent verbal efflorescences.

The following sentence is illustrative of the literary style of the work: "And here one of the weirdest whims in the universe unfolded and flashed from its burning god—the sun god of that opulent splendor of the Nile and nearer Orient—5000 years ago—to insurge into the dead the light which produced life." Surely the writer does not mean to imply that the miracle of creation occurred only five thousand years ago. Even Bishop Ussher thought it was more remote than that. But what does he mean to imply? There are many other passages just as obscure.

The reader who is able to penetrate this literary style will find that on the whole the author's thought is lucid and logical, and that its apparent esotericity is the result of the complexity of his expression and his indifferent diction. To spell the plural of nautilus as nautilae is evidence of ignorance; to refer to the cycads as cyclads is evidence of carelessness; to speak of the vitalism of lower organisms when their vitality is meant is evidence of sloppy thought. The reviewer would have preferred greater accuracy and less embellishment. Are such words as necroptic, validant, ozaric, and mirrophonic necessary in what is obviously an attempt to popularize cosmic philosophy?

Yet there is much in the book to merit commendation. One needs only recall the author's definition of fossils as "silhouettes cut by death" or his comparison of the relation between mind and body with that between time and space. It is true that his speculations as to the light that relativity physics may throw on the doctrine of immortality are after all, only speculations, but they are reasonable speculations. And if his statement that matter is a far greater mystery than mind had been remembered by the philosophers of the past they might have avoided the morass in which psychology has for so long been mired, and from which it is only now with difficulty extricating itself.

This is not the sort of book that needs an index and the author has not bothered to supply one.

SCIENCE IN CHILDHOOD EDUCATION. *Practical Suggestions for Teaching, Number 8.*

By Gerald S. Craig. Bureau of Publications, Teachers College, Columbia University, New York. $1.00 (cloth); 60 cents (paper). vii + 86 pp. 1944.

It is encouraging to see that those responsible for the character of science teaching in the elementary and secondary schools are alert to its needs. Craig directs his remarks to teachers of the lower grades. He emphasizes the importance of seizing on the natural curiosity of children and the situations that arise spontaneously in play and daily life, for motivating scientific studies. He regards the inculcation of attitudes, particularly of the openmindedness and criticalmindedness of the scientific spirit and the recognition of the importance of planning, as more important than specific content. The curriculum itself should be planned, he thinks, around the development of desirable social attitudes and behavior. Sequence and continuity should be planned in terms of the child's own growth and development. Basic principles to be taught should include: (1) the universe is very large; (2) the earth is very old; (3) changes occur continuously in the universe; (4) life is adapted to the environment; (5) living things are interdependent; (6) variation is manifested in both living and non-living things. While the child must learn to recognize that his community is but an interdependent part of a large world, community activities and resources may logically be made the center of organization of the curriculum. This subject is thoroughly illustrated with examples that should stimulate and aid the teacher.

Although somewhat wordy and repetitious, this booklet deserves a place on the shelf on every science teacher, particularly of those who teach on the elementary level.

BENTLEY GLASS

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LIFE OVERFLOWS: *An Original Scrapbook Arrangement of Soothing Philosophical Thoughts.*

By Carl Leonard Thenebe. Bruce Humphries, Boston. $2.50. 116 pp. 1944.

A physician's moralizing in prose and verse, the quality of which is sufficiently apparent from the following:

"THINK WELL OF ALL
The rule of liking all, perhaps it even hurts.
Rewards will us befall, finesse will win converts!"

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A NEW MANUAL FOR THE BIOLOGY LABORATORY.

By Bernard R. Weimer and Earl L. Core. John Wiley and Sons, New York; Chapman and Hall, London. $2.00 (paper). 213 pp. 1944.

This manual, written especially to accompany the textbooks of Strausbaugh and Weimer but designed for any elementary college course in general biology, includes approximately 50 pages of written directions and 150 pages of blanks for original drawings and outlines for labelling.

After introductory exercises with the microscope on plant and animal cells, including *Elodea* and *Ameba*, the structure of a typical angiosperm is presented. This is followed by directions for the study of food manufacture and storage in plants and then for the study in both plants and animals of digestion, food transfer, respiration, excretion, and irritability. The skeletons of the frog, bird, and man, and the muscles of the frog are considered next, followed by the reproduction of the flowering plants, the development of the frog, and, very briefly, homology. The section on heredity includes mitosis, meiosis in *Ascaris*, and simple *Drosophila* crosses. The directions end with two long sections, of necessity largely anatomical, one a survey of the plant, the other of the animal kingdom. Finally there is an exercise on ecology.

Both students and instructors will undoubtedly find this a very useful manual with many virtues. Structures are described with enough detail for the student to know what to look for. At the same time there are plenty of things left to the student, so that real demands are made on his own powers of observation. There is a reasonable degree of attention to the functional aspects of each subject, not only in the questions following each exercise, but also in the number of physiological experiments included, although the nerve-muscle section is disappointing in this respect.

There is a workable flexibility in organization which most instructors will want to utilize; e.g., it would seem desirable for students to work out the reproduction of the fern, which is given near the end of the manual in the section on the plant kingdom, before they attempt the reproduction of a flowering plant, which is given much earlier in the book. It seems strange to have the section on homology far separated from the section on vertebrate limbs, especially when it deals with limbs, albeit those of embryos. Various incidental matters need correction, e.g., pulvillus is used in place of tarsus, and fertilization is described as the uniting of "two large vesicular nuclei." The only constant confusion in using the manual arises from the purely typographical circumstance that technical terms and the numbers given to questions are printed in such very bold type that they completely overshadow the comparatively modest but much more important topical captions.

GAIRDNER MOMENT

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ECOLOGY

ZEBU-CROSS CATTLE IN NORTHERN AUSTRALIA. *An Ecological Experiment. Bulletin No. 172.*

By R. B. Kelley. Council for Scientific and Industrial Research, Commonwealth of Australia, Melbourne. Free upon request. 96 pp.; 16 plates. 1943.

This photo-lithographed bulletin recounts the results of the introduction of Zebu genetic traits into the beef and dairy herds of northern Queensland. It will be of interest not only to animal breeders, but to geneticists and ecologists as well. After a preliminary discussion of the origins of modern cattle and the respective adaptive traits of European and tropical Zebu strains, the introduction of American-bred Zebus into Australia is described, together with the several hybridization experiments that followed. The results appear highly satisfactory. In the region of Queensland north of the tropic of Capricorn, the hybrids are much more resistant to ticks and heat than cattle of pure European extraction, and make better growth and produce an equal or superior type of beef on similar pasturage. The ideal intermixture appears to be about three-eighths Zebu. The only drawback results from the higher intelligence and consequently lesser tractability of the hybrids. This is not serious. Although genetic data are inadequate for critical analysis, resistance to heat, to ticks, and to tick fever, as well as the other qualities mentioned, each appear to rest upon a multifactorial basis. Ecologically, it may be concluded that the Zebu type of cattle is genetically better adapted to tropical or subtropical habitats than European cattle are.

Bentley Glass

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Climatology.

By Bernhard Haurwitz and James M. Austin. McGraw-Hill Book Company, New York and London. $4.50. xi + 410 pp.; map and 17 plates. 1944.

This book was written to serve as an introductory text in climatology for meteorologists. It is not suitable for the general student. For students with a meteorological background, however, it is excellent.

There are two parts The first, General Climatology, deals with the elements of climatology in a thorough way. Solar radiation, temperature, wind and pressure, air masses and fronts, cyclones and anticyclones, climatic classifications, climatic types, and microclimatology are discussed.

The second part describes the regional climatology of the world. In this section the climate of each area considered is described in terms of the meteorological elements. This gives the student the "why" of each climate and makes climates a matter of reason and understanding to an extent not usually found in climatology texts. This outlook deserves to be more widely applied.

There are ample maps, charts, and tables, and a rear pocket contains seventeen loose maps of climatological data. Students should find this a most useful text.

George F. Carter

EVOLUTION

Evolution, Creation and Science.

By Frank Lewis Marsh Review and Herald Publishing Association, Washington. $2.25. 304 pp. 1944.

It is a matter of common knowledge that there are, not one, but many different theories of evolution. It is not so generally understood that there may be as many different theories of special creation. The theory expounded in this book will come as a surprise to those who are familiar with only that one based upon the postulate that there are as many species as there were originally created pairs.

Perhaps the greatest disservice ever rendered to the theory of special creation, according to the author, has been this dictum, which is of comparatively recent origin. The futility of attempting to generalize about species becomes evident as soon as one considers the various interpretations given this term by modern writers, most of whom feel constrained to distinguish between taxonomic and genetic species. To avoid this confusion the author has recourse to the Hebrew term *baramin* meaning "originally created thing," and as an example he mentions the varous breeds of dogs, which, although differing more widely than recognized species, are generally considered conspecific—an opinion in which the dogs themselves seem to concur. It is the baramin, and not any of the modern conceptions of the species which the author of Genesis had in mind when he wrote that every living thing reproduces "after his kind." Even today we speak of the cat kind, the horse kind, etc. These are all baramins, each descended from a single pair. The author of Genesis was not writing a scientific book, and to equate his terminology with that of modern science is quite unjustifiable. The author of the book under review is on solid ground when he insists that to render "kind" as "baramin" is to translate without interpreting, and so to preserve the meaning of the original text.

In rebuttal, it may be claimed that by uniting such diverse forms as the buffalo, the wisent, the aurochs, the bison, and the yak in a single baramin the author has accepted evolution in principle. But the theory that all forms of organic life have a common origin is a far cry from simple variation within each baramin. As an illustration of this difference the author discusses the many *Drosophila* investigations by modern students, with which he is thoroughly familiar. The number of mutations that may arise in a population of vinegar flies is legion, but they are never other than new forms of vinegar fly—no *Drosophila* mutant has ever been a dragon fly or a caddis fly or even a horse fly. And even the mutants that do appear are not strictly new, for they may be atavistic reversions to forms which have appeared many times in the ancestral stock. If we breed mutations long enough we can always get back eventually to the form from which we started. In other words we have variation without progression, and consequently without evolution. Here the author is again on solid ground.

Of course, the evolutionist, even though conceding that no new species has ever arisen as the result of a single mutation, can still claim that there is no reason why one should not arise from a concatenation of cumulative mutations. This theory is reasonable but it is not amenable to laboratory investigation because the human life span is too short. Even the elapsed time since the theory of evolution has been placed on a firm footing is too short for a relay of students to catch evolution "on the fly." The doctrine must be accepted on faith, because the universe as we know it is incomprehensible on any other basis. Doubtless the Omnipotent Creator could have set the cosmos going by a single divine fiat, if He had chosen to do so, but the obvious fact is that He did not so choose. The naive realist who believes only what his eyes can see or his hands can touch cannot accept the doctrine, and the materialistic philosopher who believes that the phenomena of life can be explained completely by the operation of physical and chemical laws cannot accept it consistently, although he may and often does accept it inconsistently.

The present reviewer is a confirmed evolutionist who believes the defense of special creation to be a lost cause, but he cannot dismiss this book as the fantasm of an irresponsible mind. Instead he can feel nothing but the greatest respect and admiration for Marsh, who is an acuitous and erudite student not only of biology but of the history of biological thought as well, and whose knowledge of practically all the modern work that has been done in genetics anyone might envy. The reviewer feels that the author has made a very telling point when he maintains that the fundamental cleavage plane in scientific thought is not between the evolutionists and the believers in special creation, for this plane of cleavage oscillates like a pendulum, and the belief that one generation may consider evolutionary may be thought creationistic by another. The unchanging cleavage, on the other hand, is that between the authoritarians and the experimenters, and this is true of other domains as well as of scientific thought.

The establishment of authoritarianism in science was due to the scholastic philosophers, who observed quite correctly that while contemporary scientists were in general agreement as to the fundamentals of their beliefs, the metaphysicians were tending to develop their own personal systems of thought. This seemed to indicate that philosophy was not keeping pace with science, and so they endeavored to divert the attention of original thinkers from science to philosophy, where it was felt that their talents were more needed. The result was that the scientific world through the dark ages to the time of Copernicus was dominated by the "ipse dixit" of Aristotle. In the meantime, philosophy, if not actually advancing, was at least expanding in complexity.

The authoritarians naturally tended to uphold the status quo, and innovations had to be based on rather convincing empirical evidence if they were to make their way against the accumulated beliefs of the ages. In the famous debate between Huxley and Wilberforce the latter's defense was almost exclusively authoritarian, for the theory of special creation had been in the saddle for over two centuries. Today the authoritarians are all evolutionists, and they prosecute their cause with the same vigor and the same arguments which their progenitors used on the other side three generations ago.

It was this dogmatic attitude, against which the Quaker and Huguenot blood of the author rebelled when he encountered it in his undergraduate days, that impelled the author to write this book. The present reviewer, who is of the same mixed ancestry, feels a great deal of sympathy for him. But the reviewer cannot share all the author's views, such as that the days of creation were of twenty-four hours each, for the sun whose rising and setting determine the length of the day was not created until the fourth day. Neither can he concur in the statement that there is no inconsistency between the Elohistic and Jahwistic narratives in Genesis, for the former declares man and woman coeval, while the latter speaks of the woman's costal rib origin. But he does believe it would be well if all theorists could write with the same tolerance and respect for those with whose views they do not agree, and with the same straightforward clarity of expression which contrasts so strongly with the ponderosity of verbiage and concomitant obfuscation of thought which philosophers still delight in.

The lack of a detailed index is the most serious defect of this book.

A STORY OUTLINE OF EVOLUTION.

By Charles W. Grimes. Bruce Humphries, Boston. $2.00. viii + 244 pp. 1944.

Appearing under the imprint of a new publisher and ostensibly revised, this is essentially the same book previously reviewed in this journal (vol. 13: 79. 1938), and the remarks then made may stand without essential alteration. The biological portion of the book is not up to date, and errors such as the identification of the notochord with the nerve cord are numerous. It should also be pointed out that the entire concept of evolution developed here is teleological. God (Nature, or purpose) intervenes in each and every step, not as prime cause but as immediate agent. It is unfortunate that the author's worthy ambition to show laymen how evolution and religious thought are in harmony has not been accompanied by a sounder knowledge of his subject.

BIBLIOGRAPHY OF FOSSIL VERTEBRATES 1934–1938. *Geological Society of America Special Papers, Number 42.*

By C. L. Camp, D. N. Taylor, and S. P. Welles. Geological Society of America, New York. $4.75 (paper). v + 663 pp. 1942.

This volume embodies the second part of the stupendous task of bringing together the literature of the world pertaining to fossil vertebrates. Camp and his associates included in the first volume papers published in the period 1928–1933, and the present one covers the period from 1934–1938. The bibliography is in three parts which cross-index one another: 1) a catalogue of papers by alphabetical arrangement of their authors; 2) a subject index; and 3) a systematic index. Appended is a list of the serial publications used, supplementary to that given in the first volume; and also a synoptic classification. These two volumes are a continuation and extension of the work of O. P. Hay, who published in 1902 and in 1930 bibliographies of the papers dealing with the fossil vertebrates of North America up through 1928. These, together with the yet unpublished survey by A. S. Romer of the literature of the world (exclusive of North America) prior to 1900, will give to vertebrate paleontologists an exceedingly useful coverage of their field.

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Miocene Fishes of Southern California. *Geological Society of America Special Papers, Number 43.*
By Lore Rose David. Geological Society of America, New York. $1.70 (paper). xiii + 193 pp.; 16 plates. 1943.

The specimens described in this paper represent 39 families, and were collected from the eastern and northern parts of the Santa Monica Mountains, from the Palos Verdes Hills of Los Angeles County, and from the Santa Maria Basin. Fourteen new species and five new genera are described

Parts I to III of the paper describe the fossil fish fauna from different horizons of the Los Angeles Basin. Part I: Collections of fossils were made at a number of localities on the west side of Sepulveda Canyon, Santa Monica Mountains. The fishes occur in hard siliceous sandstone and shale of the lower Modelo formation (Upper Miocene). Eighteen families and twenty genera are represented. The assemblage suggests a marine neritic subtropical fauna, living at a depth of 100 to 200 meters. Part II: The diatomaceous shale of the Upper Modelo formation was collected at localities near Van Nuys along the northern rim of the Santa Monica Mountains. The restricted fauna of a bathypelagical environment is represented by nine genera. Part III: Fossil fish are described from marine deposits of late middle to early Upper Miocene age (Altamira shale) on the coast of the Palos Verdes Hills, near San Pedro. A subtropical shallow sea is indicated at the place of deposition of this particular assemblance. Part IV: The herring-like fishes of the California Miocene are reviewed. This type of fish is the most common in the Miocene deposits. Part V: A study of the extinct family Zaphlegidae, which was related to the Gempylidae and lived in the offshore deeper water. The reasons for its extinction were possibly climatic changes toward the end of the Miocene. Part VI: A complete revision of the fish fauna from the diatomaceous earth of Lompoc, Santa Barbara County, California. The fauna comprises 31 families, 39 genera, and 42 species. It represents a harmonious assemblage that accumulated in a warm-temperate coastal sea of 25 to 50 fathoms depth, half a mile offshore. The author presents evidence that a greater similarity existed between the fish faunas of the Pacific and Atlantic coasts of America during the Miocene than at present. A relatively great number of forms has become extinct in the California sea since Miocene times.

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Hadrosaurian Dinosaurs of North America. *Geological Society of America Special Papers, Number 40.*
By Richard S. Lull and Nelda E. Wright. Geological Society of America, New York. $2 25 (paper). xi + 242 pp ; 31 plates. 1942.

The present paper is a monographic review of a group of dinosaurs which has been extensively studied, as is emphasized by the 194 titles in the bibliography. The value of a uniform approach to such a complex and interesting group of animals is obvious. The text includes the geological and geographical distribution of the hadrosaurs, and a discussion of the climate and the plant and animal environment, as gathered from the structure and fossils of the associated rocks. The major portion of the monograph is devoted to a discussion of the morphology, and a systematic description of genera and species. The skeleton is described in great detail, and with excellent illustrations. Brain casts of one species are figured, and an attempt is made to reconstruct the muscular system. The shape and size of the muscles of fossil forms are deduced from the structure of the bones to which they are attached. It is well known, of course, from a study of living vertebrates, that the presence or absence of bony ridges, fossae, spines and tubercles may often be very misleading when compared with the associated muscles. Such a reconstruction as that made in the present volume is valuable, but should be regarded in only the most general sense. The family Hadrosauridae includes, in this monograph, 23 genera (of which seven are of doubtful status) and 52 species.

* * *

Origin of Mammals Based upon Cranial Morphology of the Therapsid Suborders. *Geological Society of America Special Papers, Number 55.*
By Everett C. Olson. Geological Society of America, New York. $1.00 (paper). xi + 136 pp. 1944.

This excellent anatomical study of mammal-like reptiles is based upon serial section and reconstruction of the skulls of representatives of the suborders Gorgonopsia, Therocephalia, Anomodontia, and Cynodontia. A detailed description is given for the inner ear, middle ear, the occipital region, and the basicranial axis. Brain casts, and certain parts of the jaws, face, and calvarium are discussed. The author subscribes to a polyphyletic hypothesis of the origin of mammals. It was suggested by Romer (1940) that the therapsid reptiles stemmed from the suborder Sphenacodontia (order Pelycosauria) in the lower Permian. Olson has given additional evidence that the early therapsids developed into many lines in the Permian, each of which attained independently varying degrees of "mammalness." In other words, "each line was approaching the mammalian threshold by developing characters to be found in mammals, but developing these characters in various relationships and in different sequences temporally." The end of the Permian, over much of the world, was marked by a development of aquatic conditions, and the therapsid groups were impoverished. Four of the lines surviving the Permian-Triassic transition were potential ancestors of the primitive mammals. From these four groups (cynodonts, bauriamorphs, ictidosaurs, protodonts), and perhaps also from other similar but unknown lines, mammals arose in at least three distinct phyla (monotremes; multituberculates; and a group including the pantotheres, symmetrodonts, triconodonts, and marsupials). It remains to determine the therapsid source of each of the mammalian groups, for only vague generalities are at present possible. The results of this very significant paper have added materially to our understanding of the origin of mammals.

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THE GEOLOGY AND PALEONTOLOGY OF THE MARINE PLIOCENE OF SAN DIEGO, CALIFORNIA. PART I. GEOLOGY. *Memoirs of the San Diego Society of Natural History, Volume II.*

By Leo George Hertlein and U. S. Grant, IV. San Diego Society of Natural History, San Diego. $1.50 (paper). 72 pp.; 1 map + 18 plates. 1944.

This monograph is introductory to the forthcoming description of the marine Pliocene invertebrate fauna of the San Diego region. It describes the physiography and stratigraphy of the region, and is admirably illustrated and provided with maps. Lists of species are given for the Cretaceous, Pliocene, and Pleistocene deposits of the region.

◆

GENERAL AND SYSTEMATIC BOTANY

AMERICAN BOTANY 1873–1892: *Decades of Transition. By Andrew Denny Rodgers III. Princeton University Press, Princeton.* $3.75. ix + 340 pp. 1944.

This volume is comprehensive in the wealth of material it presents, discriminating in its selection of significant and revealing correspondence, and searching in its interpretations of the inter-relation of trends and activities in the rapidly growing field of botany.

Centering around Asa Gray as leader and pioneer, the book traces the development of a richly productive period of exploration, collection, and monographic taxonomy, with due attention to Gray's associates and to the work of the younger men stimulated by them to enthusiastic activity. Although complete in itself, the volume is most effective when read in connection with the companion biographies of Torrey, Sullivant, and Coulter, for the lives and work of the many botanists involved run from one to the other in a closely interwoven relationship. Extending out from the activities of Gray and his associates, the development of related fields is traced; the growth of paleo-botany from the pioneer work of Lesquereux; the stimulating influence of Darwin's interpretation of evolution, strengthened in its effect in this country by the staunch support of Gray; the development of botanic gardens for experimentation and research rather than for display; the rapid advance of state experiment stations and the influence of Bailey and others in gaining recognition for horticulture and other applied aspects as worthy branches of botany; the rise of the scientific laboratory approach correlated with observations and collections in the field, and the resulting advance of some of the more academic scientific phases of botany.

As in the author's other books, this is no mere chronicle of events and contributions, for the personalities of the many botanists are made vivid and living by illuminating excerpts from correspondence, giving strong support to Emil Ludwig's belief that "it is the anecdote that best reveals the personality." The chapter on the controversy between Gray and Greene significantly reveals the personalities not only of these two men, one representative of the botanical activity of the more conservative East coast, the other of the more radical West, but also of the other botanists associated with them.

If there is any criticism that may be advanced by the reader, it might be that throughout this book and its companion biographies, the interweaving of activities and influences of the many personalities and groups involved become so complicated that the reader inevitably is somewhat bewildered, yet the ample and detailed index facilitates rapid reference to any one botanist or any phase of the complicated picture, offering helpful guidance through the maze of activities, personalities, and events.

That the younger botanists of the day are more inclined to think in terms of the present and of the future is wholly natural, but reading this book and its companion volumes will bring to them the realization that they can profit greatly by these interpretive surveys of the botanical past that is their heritage. To play their part in the development of botany in the United States was the destiny of the many pioneers whose work and personalities are so ably presented in these books; to grasp, interpret, and present effectively with appreciation and understanding the contributions of these men is in itself a contribution to the science, and it would be fitting for some botanical society to make Rodgers an honorary member, since in him botany has found an interpreter, spokesman, and historian.

Wm. H. Weston

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Aquatic Plants of the United States. *Handbooks of American Natural History Volume IV.*
By Walter Conrad Muenscher. Comstock Publishing Company, Ithaca, N. Y. $5.00. x + 374 pp. 1944.

This book invites comparison with Fassett's *Manual of Aquatic Plants*, and the comparison reveals considerable differences. Although both books are profusely illustrated, so that plants can often be identified by means of the drawings, the accompanying keys are widely divergent. Fassett's key is avowedly designed for the identification of sterile plants, while the extensive use of differences in reproductive forms by Muenscher makes it impossible in many cases to identify a plant by its vegetative characters alone.

The scope of the two books also differs, in that Fassett confines himself to aquatic plants of the eastern United States, but includes all the macroscopically visible plants excepting the fungi; and Muenscher, while covering the whole of the United States, includes only Pteridophytes and Spermatophytes.

A further difference is in the classification of forms and varieties, in regard to which Fassett is a "splitter," and Muenscher a "lumper," although the latter does describe the variation within species.

Muenscher's key and his distribution map for each species are very practical, and the drawings are excellent. The book is a welcome addition to this field.

Eileen Sutton Gersh

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The Aquatic Oomycetes of Wisconsin. *Part One. By Frederick Taylor Wolf. The University of Wisconsin Press, Madison.* $1.50. 64 pp. 1944.

Under the above title, the author has collected and organized, in brief monographic form, the results of his own and others' extensive investigations of the aquatic fungi of Wisconsin. The book contains detailed descriptions of fifty-four species, ranging through six orders and twenty-two genera of aquatic oomycetes, records of their collections in the state, and keys for their identification, as background for further and more intensive work on these problematical organisms. Several plates of original drawings, and a very complete citation and summary of previous publications on the aquatic Phycomycetes accompany the work.

L. M. Langdon

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Root Disease Fungi. *A Treatise on the Epidemiology of Soil-borne Disease in Crop Plants, and a First Exposition of the Principles of Root Disease Control. Annales Cryptogamici et Phytopathologici, Volume I. By S. D. Garrett. The Chronica Botanica Company, Waltham, Massachusetts; G. E. Stechert and Company, New York.* $4.50. 177 pp.; 1 plate. 1944.

Preeminently qualified by his widely known investigations of various root diseases in Australia and Great Britain, the author here presents a volume highly valuable and significant. Although primarily concerned with the fungi attacking the root systems of crop plants, the book gives adequate recognition and careful consideration to the part played by the physiological condition of the plant and by the nature of the living and non-living components of the soil.

The introduction covers the historical background of the subject, tracing the shift in emphasis from the early preoccupation with the parasite itself to the more recent realization that such factors as temperature, acidity, and the microbiological equilibrium of the soil strongly influence the incidence and severity of root diseases, and discussing the application of this broader knowledge to their control.

Five detailed chapters discuss the parasitic activity of the root-infecting fungi, covering their specialization, methods of spread, and the influence of the soil upon them through such diverse features as temperature, moisture, texture, reaction, organic content, and concentration of nutrients.

The saprophytic activities of these fungi in spreading through the soil or in persisting in dead tissues, and their dormant survival in the soil by means of resting spores or sclerotia, are adequately covered in Chapters 7 and 8.

The remainder of the book, about one-half of its total, is devoted to a comprehensive and thorough discussion of the control of root diseases from the ecological point of view. In ecological categories of crop conditions, control is considered first in field crops by such measures as rotation, plant sanitation, and modification of the soil under the growing crop; then in plantation crops on virgin areas or on areas long planted, with also a brief discussion of special problems presented by certain types of diseases; and finally, in glasshouse crops, where more direct attack by partial sterilization of the soil is facilitated by the limited area of soil enclosed under more regulated conditions.

The nine figures, ranging from illustrations of fungus mycelium in the root tissue to maps of the spread of root diseases under different conditions of cultivation, so helpfully supplement appropriate parts of the text that one realizes the value of the book could have been greatly enhanced by more such illustrations.

A bibliography comprising nearly 450 titles ranging from the early classics, such as Woronin's 1878 paper on club root of cabbage and Thaxter's publications in 1891–92 on potato scab, to the most recent literature gives an extensive background and commands admiration for the searching work of the author in so thoroughly covering the extensive field. A general index of nine pages and an author's index of four handily expedite reference to the many phases covered in the volume.

As the first volume of *Annales Cryptogamici et Phytopathologici* the book auspiciously begins this new series, admirably maintaining in its field the high standards already established under the editorship of Verdoorn in the fourteen volumes of the companion series of plant science books previously reviewed here.

Wm. H. Weston

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PLANT MORPHOGENESIS

Organogenesis in Rubus. *University of Hawaii Research Publication Number 21.*

By Charles J. Engard. University of Hawaii, Honolulu. $3.75 (paper). xvi + 234 pp. 1944.

The reader should not be misled by this title, for the scope of this bulletin is far more extensive than might be assumed. The writer not only has made a thorough histogenetic and morphogenetic study of an entire plant but throughout the work has considered the plant as a unit, all parts of which are physiologically correlated. Motivated originally by an interest in sieve-tube structure derived from his previous studies on solute translocation in *Rubus*, the writer has followed this investigation for more than six years. The four species of *Rubus* that are the subjects of this intensive study were chosen because they are representatives of widely separated and distinctive natural localities and represent the two sub-genera recognized in this large and varied genus.

After considering such fundamental matters as the classification and gross morphology of the genus and the methods used in carrying on the work, the main body of the book comprises the detailed and thorough study of the stem apex, of the foliage leaf, of the stem, comprising vascular and other tissue systems and cells, of the root, and of the flower.

Using the approaches of the modern school of morphologists, the writer here submits an admirably thorough study of the origin and development of all tissues, organs, and appendages of the four subject species, correlating the ontogeny with physiological relationships to the organism as a whole.

Any botanist, whether or not he is of the elect who will follow with absorbed interest the wealth of technical data in the body of the paper, will profit by a careful reading of Chapter XI. This chapter, under the title "Organa Sui Generis or Organa Homologata," develops further the concept of morphology upon which the writer bases his whole study. His analysis of Goethe's conception and interpretations is the most adequate presentation that has appeared in any recent morphological treatise. His reconsideration of Goethe's theories and concepts in the light of modern research is most illuminating. His reconciliation of some of the conflicting interpretations of other morphologists shows notable breadth and vision. All in all, the scope of this volume extends far beyond an histological study of four species of one genus, its implications and bearing making it an important contribution that undoubtedly will stimulate further work in this fundamental field.

Wm. H. Weston

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PLANT NUTRITION

The Diagnosis of Mineral Deficiencies in Plants by Visual Symptoms. *A Colour Atlas and Guide. Supplement 1944.*

By T. Wallace. His Majesty's Stationery Office, London. 5s. 48 pp. 1944.

This supplement to the excellent color atlas previously reviewed (vol. 19: 341. 1944) adds 95 color plates showing the effects of deficiencies on additional crops (flax, pea, red clover, lucerne, lettuce, radish, leek, celery, pear, plum, cherry) and additional deficiencies, in particular nitrogen deficiencies, for crops previously included. An index to the combined original edition and supplement has been prepared. The original edition and supplement may now be obtained bound as one volume (15s.).

* * *

Soil and Plant Analysis. *A Laboratory Manual of Methods for the Examination of Soils and the Determination of the Inorganic Constituents of Plants.*

By C. S. Piper. Interscience Publishers, Inc., New York. $4.50. xiv + 368 pp. 1944.

This authorized photo offset, reprinted from the original published by the University of Adelaide, Australia, in 1942, greatly extends the sphere of usefulness of this handy volume. A highly practical book designed to serve as a technical laboratory manual, it will prove directly useful to agricultural chemists and others whose field of work touches either pedology or plant analysis, since the book comprises the methods in actual use in the laboratories at Waite Institute, where the author has worked as chemist for nearly twenty years.

Part I, comprising about two-thirds of the book, is concerned with methods for the examination of soils, and follows in detail all of the steps involved from the collection of the soil samples in the field and their preparation in the laboratory through the many types of precise and exacting analyses. There are detailed discussions of suitable procedures for the determination of hydrogen-ion concentrations and of conductivity; methods of mechanical analysis of water-holding capacity; the determination of calcium carbonate, analysis of the hydrochloric acid extract, and determination of the exchangeable ions. Determination of nitrogen, nitrates, nitrites, and ammonia as well as of organic matter is well treated, and the separation of the clay fraction, with the determination of silica, iron, and alumina, is adequately covered.

Part II, in approximately 100 pages, presents the methods for the determination of the inorganic constituents of plants, covering the preliminary steps such as the collection and preparation of samples and the various approved methods for ashing, and the precise procedure for the determination not only of the commoner inorganic constituents but also of the trace elements.

The illustrations, in 19 line cuts, helpfully depict some of the essential apparatus used, giving details of assembly and construction. Pertinent references follow each chapter so that no assembled bibliography is necessary. Adequate subject indices, one for soil analysis and another for plant analysis, complete the book.

A thoroughly practical and usable manual, the book will prove a valuable tool in its technical field, a field in which relatively few such comprehensive guides are now available.

Wm. H. Weston

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ECONOMIC BOTANY

The Peats of New Jersey and Their Utilization. *Part B of The Peat Resources of New Jersey. Bulletin 55—Part B, Geologic Series, Department of Conservation and Development, State of New Jersey.*

By Selman A. Waksman, H. Schulhoff, C. A. Hickman, T. C. Cordon, and S. C. Stevens. Department of Conservation and Development, State of New Jersey, in cooperation with New Jersey Agricultural Experiment Station, Rutgers University; Trenton. $1.00 (paper). 278 pp. 1943.

This report on the quantity, availability, and quality of the peat deposits of New Jersey was prepared for the purpose of aiding the exploitation of these deposits as a valuable natural resource which had become increasingly important in the state for replacing the peat formerly imported from the Scandinavian countries and Germany. Since about 70 per cent of the peat areas in the state were carefully surveyed, and this percentage was representative in nature and distribution, adequate information was secured for generalizations as to the total resources. The distribution of these deposits and their area, depth, and availability for exploitation are considered, as well as the quality and the botanical and chemical nature of peat itself. The thoroughness and comprehensiveness of the survey is apparent even from the introductory presentation of the plan followed and the methods used.

Chapter I covers fundamental matters involved in the geography, geology, and topography of the peat lands. These are not inconsiderable, since they occupy about 20 per cent of the undeveloped land of the state. Especially interesting to the biologist is the discussion of the vegetation factors involved in peat formation, with pollen analyses of representative bogs and studies of the associated calcareous marl formations.

Chapter II covers the properties, nature, and distribution of the peats in their more general aspects through the 21 regions into which, for the purposes of this survey, the state was divided, according to drainage basins and the bog, swamp, and marsh areas.

The body of the bulletin, comprising 158 pages, presents in three successive chapters detailed information on the three regional types of peat deposits: the northern, predominantly of the reed and sedge type; the coastal plain, predominantly of the forest type; and the salt marsh and alluvial types. The material in these three chapters, representing the carefully studied data accumulated in more than three years' work, is detailed and comprehensive in itself and is amplified by a wealth of illustrations in 15 plates and 42 figures comprising maps, cross-section diagrams, and photographs of ecologic associations.

The final chapter, on the utilization of peats in New Jersey, surveys the use of tidal marshes reclaimed for agriculture by diking and draining for pasture and hay or for growing cranberries, blueberries, or certain suitable truck crops; the "mining" of buried cedar logs still profitably carried on after nearly 200 years of exploitation; and the direct uses of peat itself for such purposes as the improvement of soils. It is interesting to note that the peat is almost all of the sedge and reed type or of the forest litter deposit type, since moss peat, resulting from long accumulation of sphagnum in quantities suitable for large scale development, is practically lacking in the state, although some surface sphagnum in the bogs is available and has been exploited on a small scale. The availability and use of so-called "orchid" peat, which consists of the fibrous roots of the osmunda or cinnamon fern, is touched on briefly, while as an example of the use of leaf mold the production at one nursery is reported as having increased from 10 tons in 1939 to over 600 tons in 1941.

A bibliography of 110 titles, containing pertinent publications from 1765 to the present, and an adequate subject index of four pages complete the book.

After appraising the possibilities for peat utilization outlined in chapter VI and its potential value to the state, the reader cannot but wonder whether this project #65-1-22-477 of the WPA—lasting over three years and employing at one time a staff of over 150 persons, comprising three state and four district supervisors, 15 to 25 field crews of five men each, an office staff of clerks, draftsmen, typists, and an artist; a laboratory staff of chemists, assistants, and laborers; and a production staff of authors, experts, collaborators, and statisticians,—accomplished results that will yield the state a return commensurate with the expenditure. There is no doubt, however, that this bulletin should stimulate an influx of botanists and seekers of the unusual, for, quite in addition to the rich and interesting collecting grounds described, such alluring names as Buckshutum Swamp, Great Egg Harbor, Jenny Jump Mt., Ongs Hat, Pimple Hills, Assanpink region, Pochuck Creek, Kittatinny, Pocanoc, Tuckahoe, Allamuchy, and Wawayanda will make even the least impressionable reader wish to fill up the old car with gas and start on extensive exploring trips as he might have in the luxurious days when this survey was made.

Wm. H. Weston

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Forestry on Private Lands in the United States. *Duke University School of Forestry Bulletin 8.*

By Clarence F. Korstian. Duke University, Durham, N. C. $1.50 (cloth); $1.00 (paper). xiii + 234 pp.; 20 plates. 1944.

The status, problems, and prospects of private forestry in the United States, as revealed in an extensive and impartial survey of eight important timber states of this country, are discussed and summarized in this report in a consideration of measures essential to the application of better forestry practices to privately owned forest properties. Adequate Control of Forest Fires, Extension Forestry, Farm Forest Cooperatives, Forest Lending Agencies, Cooperative Research, Forest Taxation, and Public Control of Cutting Practices are some of the important subjects dealt with by an authority on these questions; as also legislative and administrative measures necessary to insure constructive forestry programs on private lands. An Appendix with a section on "Forest Terminology," and a carefully prepared bibliography of over 150 titles constitute a further valuable contribution.

L. M. Langdon

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Commercial Flower Forcing. *The Fundamentals and Their Practical Application to the Culture of Greenhouse Crops. Fourth Edition.*

By Alex Laurie and D. C. Kiplinger. The Blakiston Company, Philadelphia. $4.50. viii + 598 pp. 1944.

While this is a practical manual for the florist and greenhouse man, it contains an abundance of information that will be most useful to professional botanists. The new edition includes a chapter on gravel culture, and desirable nutrient levels for greenhouse crops are given in tabular form. Soil sterilization, fertilizers, temperature control, the importance of humidity, use of growth promoting and root-forming substances, methods of propagation, and new measures of pest control are but a few of the valuable topics considered. The chapter on greenhouse construction and heating should be very useful to departments considering new construction. The section dealing with individual crops will also be of value. The book is to be recommended as a standard manual for all botany and biology departments equipped with greenhouses, and to all flower growers, whether for profit or pleasure.

GENERAL AND SYSTEMATIC ZOOLOGY

An Introduction to Animal Biology. *Second Edition.*

By John B. Parker and John J. Clarke. The C. V. Mosby Company, St. Louis. $3.75. 532 pp. 1945.

The second edition of this textbook on animal biology has been revised and brought up to date, although the essential contents and manner of presentation have not been altered. The authors have written the subject to make it serve as a means to teach the student, and to illustrate and correlate the information garnered in the lecture room and the laboratory, and not as a reference text loaded with data not essential to the general biology student. With this view in mind, the volume has indeed been well written and should serve the purpose for which it is intended. Many of the illustrations are original, which is a fact always to be admired in college zoology texts. There is a suitable index and a good glossary.

Henri C. Seibert

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Atlas in General Zoology.

By Alfred M. Elliott. Published by the author, State Teachers College, Bemidji, Minnesota. $1.20 (unbound). 62 plates. 1944.

This envelope of loose-leaf drawings has been prepared by the author to appeal more widely than do standard illustrations to those students whose major interest lies outside the field of biology. He has certainly succeeded in being graphic and interesting. The diagrams are outstanding in clarity, details having been sacrificed for principles. Three-dimensional effects are used, humor is skilfully and appropriately introduced, and the order of artistry is high. The style of illustration is very reminiscent of that used in Buchsbaum's *Animals Without Backbones*, and the similarity in some instances raises a wonder as to why acknowledgment has not been made.

Only a single doubt intrudes in the reviewer's mind. Will the student who is given these plates tend to rely upon them overmuch? Will there not be a temptation to make them a substitute for the accurate, painstaking observation of objects in the laboratory, and the effort to delineate them, that together are so important in teaching the methods and spirit of scientific inquiry? If this danger can be avoided, the atlas should be a very worth-while teaching aid.

BENTLEY GLASS

INTRODUCTION TO PARASITOLOGY.

By A. S. Pearse. Charles C. Thomas, Springfield, Illinois; Baltimore. $3 75. ix + 357 pp. 1942.

A tremendous amount of information is condensed into this little volume. It represents a survey of the entire animal kingdom for parasitic organisms. It is not intended to be an exhaustive presentation, but the forms discussed are certainly numerous and varied. Although the book is broad in its scope, it does stress the parasites of man. For instance, entire chapters are devoted to malaria and hookworm, inasmuch as they are particularly important in the United States. However, most of the human forms are treated rather superficially and, sometimes, none too accurately. Despite the emphasis on the human forms, the greatest majority of the organisms discussed never attack man. Nevertheless, many of them do not lack human interest, since they are economically important because of their attacks upon wild and domestic animals that man uses as food.

Pearse has planned the book to furnish reference material to supplement lectures and laboratory work, and not as a textbook adapted to reading assignments. As he has expressed it, "it is hoped that it will be useful in 'looking things up,' whether it is used in a class room, on a farm or a fishing boat, in a packing house or a seaside laboratory." It will no doubt find a place on the reference lists of courses in general biology, invertebrate zoology, and ecology, as well as on those in introductory parasitology.

Due to the reference nature of the book, much of it is not very readable. However, scattered among the concise morphological descriptions are fascinating bits of information on parasitism—the fish that deposits her eggs inside of clams; ants that obtain most of their food from the tongues of other ants that are their slaves; the minute fish that swims into the urethra of man; birds that lay their eggs in nests of other species; and countless others. Other interesting portions of the book concern the evolution of the parasitic habits of the various organisms.

The text material is profusely illustrated with clear-cut line drawings. The reviewer is by no means acquainted with all of the forms pictured, but the poor illustrations of some of the human parasites makes him wonder if the figures of the non-human forms are adequate for correct identification. The drawing of the malarial parasites (fig. 77) is exceptionally poor.

One chapter is devoted to the methods of examining fecal samples for intestinal parasites. The different procedures of concentrating and enumerating such organisms are discussed briefly. In this discussion the author expresses the attitude of the "true" parasitologist, which is sometimes difficult for others to appreciate. "The examination of feces day after day might be thought to be tiresome routine, and it is certainly malodorous!; but when it is to furnish data which may be used to change the lives of whole communities and nations, it becomes interesting and exciting. For a parasitologist the discovery of a worm egg, an amoeba cyst, or a malarial parasite gives more pleasure and satisfaction than a fisherman gets from catching a fish or a hunter from shooting a duck. It is real sport!" More technique is presented in the last chapter. The author summarizes methods of collecting, preserving, staining, and mounting parasitological specimens. It is divided according to the major taxonomic groups in order to emphasize the techniques particularly applicable to specialized structures.

M. M. BROOKE

DEVESCOVINID FLAGELLATES OF TERMITES. IV. THE GENERA METADEVESCOVINA AND PSEUDODEVESCOVINA. *University of California Publications in Zoology, Volume 45, No. 4.*

By Harold Kirby. University of California Press, Berkeley and Los Angeles. $1.25 (paper). Pp. 247–318; plates 32–44. 1945.

In this fourth in the series of monographic treatments of devescovinid flagellates, sixteen species of *Metadevescovina*, thirteen of them new, and four species of *Pseudodevescovina*, none new, are described. Drawings are given of each species. Particularly interesting are the varied forms taken by the axostyle and parabasal body. All the species of *Metadevescovina* except one are confined to a single family of the termite host. *Pseudodevescovina* is reported only from the genus *Neotermes* in Australia and Africa.

HANDBOOK OF THE MOSQUITOES OF NORTH AMERICA. *Their Anatomy and Biology; how they can be studied and how identified; how they carry disease and how they can*

be controlled. Second Edition: Revised and Amplified.
By Robert Matheson. Comstock Publishing Company, Ithaca. $4.00. viii + 314 pp. 1944.

For untold centuries, mosquitoes, with their insidious desire for fresh blood, have plagued man and beast to such an extent that in some areas coexistence has been made unbearable if not impossible. Although they still rate as notorious pests, the great attention that is now focused upon them is primarily due to their ability to transmit certain diseases. In North America, there are four important human diseases that are known to be transmitted only by mosquitoes—malaria, dengue, yellow fever, and filariasis. These same diseases are even more prevalent in many parts of the world where our service men are now stationed. Undoubtedly, numbers of them will acquire infections and return to this country, where the stage is already set for transmission. Furthermore, exotic strains of these diseases may be introduced which might intensify the situation. It is therefore, particularly important and timely that Matheson should present a revised edition of his valuable handbook. It is his hope that by making authoritative information readily available, those concerned with the public health of our country will be able to correctly identify the medically important mosquitoes and thus be in a position to institute more effective methods of control.

The present edition is organized on the same pattern as the first. There are two major divisions; the first part deals with the more general aspects of the subject, and the more extensive second part presents a systematic account of the North American mosquitoes. Many of the chapters have the same titles and subheadings, but inasmuch as the first edition appeared over fifteen years ago, much revising and amplifying has been necessary. The following are a few of the changes and additions that appear in the revised edition. Thirteen species of *Anopheles* are presented instead of eight; *freeborni*, *bradleyi*, *georgianus*, *ablimanus*, and *franciscanus* having been added. Within the tribe Culicini, *Mansonia* is now presented as a separate genus, *Taeniorhynchus* is considered as a synonym of *Aedes*, *Culiseta* has gained priority over the term *Theobaldia*, and *Megarhinus* has been removed from the Culicini and placed in a separate tribe, Megarhinini. Whereas originally the Chaoborinae were barely mentioned, a new chapter is now devoted to this subfamily of the Culicidae. New keys to the genera and species have been written, and nearly twice as many plates and figures illustrate the text material.

By means of intelligible keys, the author leads the reader from the family Culicidae of the order Diptera down through the taxonomic subdivisions to the various genera and species. In many instances, keys are given for three stages of the mosquitoes, larvae (4th instar), pupae, and adults. No attention is given to the characteristics of the eggs and first instar larvae. For the adult stage, the characteristics of the male genitalia are extensively used. The author also presents brief discussions of each of the species found in the keys. In these discussions, the synonyms are mentioned, and references are made to the literature containing the original descriptions. For the important species, the discussions present the diagnostic characteristics of the various stages, their known distribution in North America, and information on their biological habits.

An index is presented, as well as an extensive list of references. These references are conveniently divided into "general works," "mainly biological," "mainly taxonomic," and "mosquito control."

M. M. Brooke

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A Review of Studies on the Mexican Fruitfly and Related Mexican Species. *United States Department of Agriculture Miscellaneous Publication No. 531.*
By A. C. Baker, W. E. Stone, C. C. Plummer, and M. McPhail. U. S. Government Printing Office, Washington. 35 cents (paper). 155 pp.; 10 plates. 1944.

This publication summarizes the results of studies conducted in Mexico by the laboratory of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture, located in Mexic City. The fruitfly *Anastrepha ludens*, is a native insec of Mexico, attacking chiefly the citrus and the mango, which were introduced many years ago. The most commonly favored native host is the yellow chapote (*Sargentia greggii*). The results obtained and the conclusions derived from laboratory experiments, from field investigations, and from published material are presented in detail. The economic aspects, such as the disposal of infested fruit, prevention of infestation, poison sprays, methods of trapping and counting populations, are naturally stressed. No definite conclusions with regard to control have apparently been reached.

There are other fruitflies in Mexico, and their identification in some instances is difficult. The shape of the ovipositor has been found useful as a diagnostic character, as well as various anatomical structures in the larvae. It is interesting to note that in many instances, differences in biological habits have later been associated with forms that have proved to be taxonomically distinct on careful reappraisal of their external morphology.

Henri C. Seibert

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The Molluscan Family Planorbidae.
By Frank Collins Baker. Collation, Revision, and Additions by Harley Jones Van Cleave. University of Illinois Press, Urbana. $14.50. xxxvi + 530 pp. (including 141 plates); 1 portrait. 1945.

The value of a taxonomic monograph is determined largely by four factors, which may be summarized briefly as contribution, collation, convention, and availability. In this one, besides studies of the shells, with figures of most American forms and of examples of all the genera, the author has contributed careful descriptions of the detailed structure of the animals, with notes on nidification and development, all well illustrated in some 75 plates. These results of long and ardent years of dissection and study form a permanent record, and this book will remain an indispensable reference, long after new studies may have outmoded its systematic decisions. A chapter on general ecology includes a discussion of the planorbids as intermediate hosts for flukes.

The abundance of new data has been collated, with that from the past, into a revision of the family. After removal of the Bulinidae, the Planorbidae are divided into the Planorbinae with twelve genera, the Segmentininae with eleven, the Helisomatinae with seven, and the Planorbulinae with four genera. Definitions, lists of the (unindexed) "valid" forms, and notes on geographic and geologic distribution are given for each genus and subgenus. In addition, Lake Baikal's *Choanomphalus*, the mutative *Poecilospira*, *Indoplanorbis* (Bulinidae), and two genera "wrongly referred to Planorbidae" are discussed. The content of these groups, in terms of the affinities of the included individuals and minor entities, and their relationships, expressed in classification, give proof of the careful inductive reasoning and mature scientific judgment of the author.

In contrast to their content and relationships, the mere sizes of taxonomic groups are largely matters of convention, utility, and opinion. F. C. Baker here, as throughout his lifetime, frankly ranks himself with the "splitters," but even those colleagues, who may not agree with his opinions, must admit that his ability to see differences requires much more care and experience than does indiscriminate "lumping." A genus, two subgenera, nine species and seventeen varieties are described as new. In main, the legal conventions of nomenclature are respected, although *Menetus callioglyptus* (Vanatta, 1895) is included in *M. cooperi*, a "new name" in 1940.

My principal criticism is that the availability of this wealth of material is impaired by the inadequate indices, which exhibit a want of taxonomic experience, because of F. C. Baker's untimely death. But, despite this, Van Cleave, with his readable biography, careful bibliography, and excellent portrait, has constructed a fitting memorial to an eager searcher and a delightful friend.

Horace B. Baker

Reptiles and Amphibians of Minnesota.

By W. J. Breckenridge. The University of Minnesota Press, Minneapolis. $2.50. xiii + 202 pp. 1944.

It is a genuine pleasure to be able to aid in introducing a new state herpetology. This is one of the best reports that has appeared and emulates Conant's very excellent account of the Ohio reptiles (Conant, Roger. 1938. The reptiles of Ohio. *Amer. Midl. Nat.*, 20(1): 1–200). The book is designed for amateurs and for advanced students of herpetology; both should find in it much of interest.

A great deal of material is incorporated into the excellent Introduction, which includes sections on the following: history of Minnesota herpetology; debunking false stories; physical features of Minnesota; collecting methods; care of reptiles and amphibians (written by Milton Thompson); snake bite treatment; methods of preservation; classification; and keys with a description of their use. Following the Introduction is a Hypothetical List, which contains a discussion of those species which had previously been erroneously reported as occurring in Minnesota, and those which have not yet been found in the state but whose occurrence may reasonably be anticipated. The main body of the book is devoted to accounts of the separate species, which usually contain the following information: common name; scientific name; races occurring in Minnesota; description; range; habits and habitat; food; breeding; and one or two references for suggested reading. Each account is usually accompanied by an illustration and two small maps. The smaller map is of North America and shows in a general way the complete range of the form. On the larger county-outline map of Minnesota, in addition to certain vegetation features, the known range of the species is shown by counties. The book is concluded with a glossary, a bibliography, and an index.

The book is readable and the illustrations are acceptable. Especially to be commended are a couple of semi-diagrammatic scale drawings of frogs that should prove to be completely sufficient for accurate identification. Although the book is a very good one and will be useful to a great many persons, there is yet much to be criticized. Breckenridge has elected to treat the Minnesota herpetofauna on the species level. Each account is hence of a full species, and if more than one subspecies occurs in Minnesota this is noted under the heading, "races." Little attention, except in the case of *Thamnophis sirtalis*, is given such matters, and the result for the novice is bound to be one of confusion. For example, the form of the newt that occurs in Minnesota is *Triturus v. louisianensis* (this is correctly stated by Breckenridge) yet the legend under the figure accompanying the account is *Triturus viridescens*. The same situation is true for the genera *Pseudacris*, *Eumeces*, *Diadophis*, *Opheodrys*, and *Coluber*. Not only will this treatment trouble the amateur but it will also disappoint herpetologists. One of the many functions of a state report should be to define the status of races within the state and map the areas of intergradation. Investigators planning generic revisions often look to these reports for such material, as they are rarely as familiar with the fauna as the author of such a manual is.

The keys (p. 27) contain some factual errors. In distinguishing between amphibians and reptiles it is stated that the former have a cartilaginous skeleton and the latter a bony skeleton whereas, of course, they both have a bony skeleton in common with all the air-breathing vertebrates. It is stated that lungs are well-developed in adult amphibians, although it is well known that in the Plethodontidae (an example of which occurs in Minnesota) the adults are lungless and depend upon cutaneous respiration for gas exchange. The statement (p. 73) that the color of the tree frog "is adjusted to blend remarkably well with its immediate surroundings" is open to question. Errors of this type are regrettable since they foster, in a few experimental zoologists, the attitude that some museum workers may be naturalists but are not biologists.

The book is good looking and typographical errors are very rare. It is to be hoped that a second edition will be warranted and that it will be sufficiently revised that the above remarks and other minor criticisms will no longer be pertinent.

ARNOLD B. GROBMAN

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AMPHIBIANS AND REPTILES OF THE CHICAGO AREA. *By Clifford H. Pope. Chicago Natural History Museum, Chicago.* $1.75 (paper). 275 pp.; 12 plates. 1944.

All the publications of Clifford Pope are interesting reading and deserve the favorable reception they have been accorded. This book will prove to be no exception and will be highly regarded, along with his popular books on the snakes and turtles of the United States, his series of technical papers on the Appalachian salamanders, and his scholarly 600-page volume on the reptiles of China.

Here one finds a detailed yet readable treatment of the salamanders, frogs, toads, lizards, snakes, and turtles of the Chicago area, in which is included those parts of Michigan, Indiana, Illinois, and Wisconsin which border the southern tip of Lake Michigan and are within a seventy-mile radius of Chicago. After an all too short introduction, the amphibian and reptile groups are briefly considered, and the forms within each are discussed in adequate detail.

Carefully simplified keys for identification are provided. Technical terms are reduced to a minimum, and those that are used are satisfactorily defined, often with diagrams, where they first appear. Also aiding in identification are the many excellent drawings of the amphibians and lizards, the photographs of the snakes, and the beautifully executed colored plates of the turtles. From the front cover, coming out to meet the reader, is a Walt Disney Tiger Salamander. The same salamander may again be seen as it leaves the reader and enters the book through the back cover.

For each form included the following information is usually supplied: common name; scientific name; references to accompanying illustrations; a section on recognition which often includes the means of distinguishing it from species with which it has a strong superficial resemblance; a section describing differences between males and females; and sections on reproduction, growth and age, habits, food and feeding habits, enemies, economic importance, habitat, captivity, and occurrence. Under the last are given both the general distribution of the form and those counties of the Chicago area from which it is already known. In this regard another reviewer (Price, John W., *Sci. Monthly*, 60: 399–400, May 1945) has suggested more distribution maps and has decried the lack of specific locality records. In my estimation of readers' requirements and the efficient utilization of space, it seems that Pope's presentation would not be improved were the above suggestions incorporated. Concluding the account for each form are one or two annotated references.

The design of this book, "written for those already interested in natural history," should prove to be highly satisfactory both to the novice and the experienced herpetologist. Terminology is given careful attention, and with almost every statement there is an indication of its source. It is unnecessary to point out the ways in which this book will be found acceptable to the interested amateur, for it has apparently been successfully organized with his requirements foremost in mind. The more serious student of amphibians and reptiles will be pleased with the wealth of information that has been brought together. Discussions of intergradation, allocation of questionable specimens, and habitat preference are woven into the species accounts. The paragraphs on life histories and habits are very well done; those on courtship and reproduction are, perhaps, overdone. There is an extensive index.

The book is preeminently satisfactory and there is little to criticize. The paper and type have been well chosen and there is an absence of typographical errors. There is no bibliography, and all references in the text are limited to the names of investigators without mention of date or journal. The addition of a glossary and a section explaining the use of the keys would make the book more useful to the inexperienced naturalist.

ARNOLD B. GROBMAN

AMERICAN BIRD SONGS.

Recorded by the Albert R. Brand Bird Song Foundation, Laboratory of Ornithology, Cornell University. Comstock Publishing Company, Ithaca, N. Y. $6.00. 6 10′ records. 1944.

The recording of these 72 bird songs in the field was a feat of tremendous technical difficulty, and all students of birds will welcome them. They stand far above all previous efforts at recording, revealing the great technical advances that have been made in recent years. This is not to say, however, that the records are perfect and will satisfy the eager desires and sharpened criticism of all bird lovers. It is difficult to judge their quality objectively, since the reproducing instrument is a variable factor of considerable importance. However, after listening to them repeatedly on a good instrument, a few criticisms appear obvious. Variations in volume from song to song on the same record face are often great and make it difficult to keep the volume adjusted; technical monitoring could be improved. The repetition of the recorder's "plug" at the beginning of each disk soon becomes wearisome. The sparrows fare better in the recordings than most other groups. Whip-poor-will and chuck-will's-widow are fine. Yet some of the most familiar songs seem least recognizable—this is true of robin, catbird, mockingbird, and flicker. The tones seem over-harsh, short of their natural lovely liquidity; the songs are atypical, and a beginner could hardly learn to identify these birds from their recordings. Others are recorded admirably--the Canada geese calling, apparently in flight, are enough to make any hunter feel a keen pang of nostalgia. Others are rare or unusual and represent outstanding inclusions: the veery, the hermit thrush, the woodcock, the chachalaca. One entire record is devoted to birds of the West, with a few additional western birds, such as Gambel's quail and the California quail, on other records. The drumming of the ruffed grouse and the calls of dusky grouse and prairie chickens, and the gobble of the wild turkey contribute exciting moments. In spite of the fact that perfection in bird recording is still to be achieved, this album will richly reward all ornithologists and bird lovers.

BENTLEY GLASS

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BIRDS OF THE SOUTHWEST PACIFIC. *A Field Guide to the Birds of the Area between Samoa, New Caledonia, and Micronesia.*

By Ernst Mayr. The Macmillan Company, New York. $3.75. xx + 316 pp.; 3 plates. 1945.

As a result of the war in the Pacific Area, museums have been flooded with requests for information on the flora and fauna of the far-flung and exotic islands by individual service men. Queries on bird life have been especially frequent, but most of the information lies scattered in technical journals and special reports not accessible to the fighting man. In response to the demand, Mayr has written this handbook of birds to be found in the following islands: Samoa, Fiji, Tonga, New Caledonia, Loyalty Islands, New Hebrides, Banks Islands, Santa Cruz Islands, Solomon Islands, Marshall Islands, Carolines, Marianas, Palau, Yap, Guam, Gilbert and Ellice Islands, and the Phoenix Islands.

In setting up a plan of presentation, the author has had quite a different problem confronting him than is met with in similar types of faunal handbooks. The area encompassed is tremendous, consisting of thousands of diversified and partially isolated islands. Furthermore, although the avifauna in a taxonomic sense may be well known, very little information is at hand on field identification, habits, and habitats. Lastly, the birds in many instances are vastly different from those that a North American ornithologist might be acquainted with. The author has resolved these difficulties very cleverly. The book is divided into two parts, the first of which describes the seabirds of the Southwest Pacific, the shorebirds, and the land and fresh-water birds. Since the first two groups consist of birds rather cosmopolitan in habit and distribution, they are described only once and their distribution recorded. But in the third group, in order to acquaint the student with the families peculiar to the Australian region, there is given a short description of each of the families found in the Southwest Pacific. Included in this section are species of widespread distribution (occurring in three or more of the seven geographical subdivisions). Part two is the geographical section listing the birds of the seven subdivisions.

Field keys are given when it is believed they will be of value in identification; color plates and black and white drawings include characteristic species of that region. The entire volume is a creditable piece of workmanship that will be of value not only to persons in the Southwest Pacific but also to others interested in the avifauna of these islands, either professionally or otherwise. The value of some of the features used in the keys as diagnostic recognition marks may be questioned; perhaps a few more illustrations might have been more helpful. But as the author continually points out, field information is scanty, and he encourages any information from those who use the book. The introduction contains hints to observers on the type of data that is badly needed.

HENRI C. SEIBERT

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WOODCOCK.

By John Alden Knight. Color plates from paintings by Edgar Burke. Alfred A. Knopf, New York. $4.00. x + 161 + ii pp.; 16 plates. 1944.

The twilight flights of the male woodcock rank fairly high among the striking courtship displays of birds, and are relatively well known; but even of those who have watched this performance, few know much about the rest of the woodcock's exceedingly private life.

This book, though it makes no claim to be a scientific study, does contribute considerably to our knowledge of the bird's habits. It discusses such surveys and preliminary banding experiments as had been carried out by the U. S. Fish and Wild Life Service and State Game commissions before the war, and states clearly what is known and what remains to be discovered about the seasonal cycle and migratory movements of the woodcock. Years of first-hand observation have enabled the author to sift facts from sportsmen's tales, and his conclusions about the type of cover selected by the woodcock are particularly interesting.

As his observations were made primarily in the capacity of a hunter, the author devotes a considerable part of the book to reminiscences of woodcock shooting and discussion of equipment and technique. There are some good illustrations of the bird and its haunts.

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Summary of the Collections of Amphibians Made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. *Proceedings of the United States National Museum, Vol. 95, No. 3185.*

By Edward H. Taylor and Hobart M. Smith. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 521–613, plates 18–32. 1945.

Results of Feeding Ether Extracts of Male Supplementary Reproductives to Groups of Nymphal Termites. *University of California Publications in Zoology, Volume 49, No. 9.*

By E. A. Keene and S. F. Light. University of California Press, Berkeley and Los Angeles. 25 cents (paper). Pp. 283–290. 1944.

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ANIMAL EMBRYOLOGY

The Embryology of Behavior: *The Beginnings of the Human Mind.*

By Arnold Gesell, in collaboration with Catherine S. Amatruda. Harper and Brothers, New York and London. $5.00. xix + 289 pp. 1945.

"He who sees things from their beginnings," quotes Gesell in the first paragraph of his *Embryology of Behavior*, "will have the most advantageous view of them." Accordingly, in compliance with the admonition of Aristotle, the author has made a brave attempt to trace the human mind to its ultimate embryonic origins.

Gesell has borrowed liberally, from the appropriate authorities, pertinent data concerning early human development. He has devoted nine of his fifteen chapters, over half his textual pages, in fact, to epitomizing and interpreting these for his readers, concentrating his attention on the development of structure and function in the motor and coordinatory apparatus, and particularly on the mechanisms regulating the breathing, tonic, and integrative processes. He has then presented, in three chapters, his original observations on the development of behavior in premature as compared with full-term infants. In his final three chapters, he has concluded by attempting to derive from the material presented a unifying concept synthesizing biological and psychical phenomena into a single scheme of things entire. At the end of the text follow forty-four plates representing "a photographic delineation of behavior patterns and growth sequences" in premature and normal infants, and two brief appendices elucidating a few of the more technical aspects of the author's original investigations.

In his treatment of data borrowed from biology, embryology, and neurology, the author is on the whole accurate and sound. In his adoption of interpretations and concepts, rather than facts, from cognate fields, he is open to reproach only for his own lack of critical skepticism. The concepts of metabolic gradients, of electrodynamic fields, of electrotonic integration, are convenient ways of describing in fresh terms physiological phenomena already familiar in other guises. Whoever accepts them unreasoningly as more than descriptive in scope runs the risk of confounding cause with effect; the critical scientist cannot accept them as ultimate explanation. Gesell, however, in appropriating these concepts, is no more at fault than the great majority of biologists and physiologists, who are themselves unfortunately still all too eager to grasp after such pale phantoms of truth.

The present reviewer is perhaps not wholly competent to evaluate the worth of the author's original contributions. The corpus of data, as presented in this volume, however, seems a little thin against the rich background of borrowed materials, and in some ways as insubstantial in structure as those happy pavilions in Flushing which neighbored Dr. Couney's excellent hospital where the basic facts were collected. The chapter describing the development of the "diurnal cycle of sleep and wakeness" is decisively analytical and intensely interesting. The descriptions of the development of other behavior patterns may be adequate in their fashion, but they lack the scientific precision and objectivity of observation and of expression that distinguish, for instance, the developmental studies by Davenport Hooker.

This deficiency may be partially accounted for by the author's predilection for playing with words, a practice in which he indulges too freely. To this reviewer, for instance, the word "growthsome," the terms "semi-demi drowsing" and "micro-munching," the phrase "genes, arranged warp-woof-wise in chromosomes," although admittedly expressive in a lyrical sort of way, are still objectionable. Gesell's style is good, but it is not that of his heroes Coleridge and Melville—nor even that of Sherrington—and might better not have succumbed even spottily to their literary influence.

The final synthesizing chapters, especially, are weakened by the author's experiments with language. He has used in his text the phrase "a kind of cauliflower overgrowth," and the simile might be extended to cover the manner in which he shrouds relatively simple ideas with a plethora of words. Experimental embryologists who have transplanted organizers, for instance, may resent being told by Gesell that their experiment "demonstrates the profoundity [sic] and inveterateness of the creative essence of growth." Nor does the author necessarily enrich the existing body of knowledge by conceiving of the development of behavior as governed by the seven principles of "individuating fore-reference," "developmental direction," "spiral reincorporation," "reciprocal interweaving," "functional asymmetry," "self-regulatory fluctuation," and "optimal tendency." Surely these principles could be more simply stated, to the greater benefit of the scientist who might choose to employ them in his own thinking.

But if Gesell's scientific effort seems a trifle shallow, and his literary phraseology over-elaborate, on the philosophical level he stands above reproach. He has followed the current fashion of thinking in terms of levels of integration, and has developed a concept of a "hierarchical continuum" in which behavioral and psychical phenomena are directly, through their development, related to physical phenomena of a lower order. By so incorporating the properties of mind and matter into a single continuous system, he localizes the mind into a position in nature in which it can be analyzed by the established methods of science. The Trylon and Perisphere have vanished, in whose shadow the Doctor's subjects squinched and munched; but by thus emphasizing on an embryological basis the fact that the human mind can be rendered scientifically comprehensible, Gesell helps to hold open the way to a more fruitful future World of Tomorrow.

JANE OPPENHEIMER

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EXPECTANTLY YOURS. *A Book for Expectant Mothers and Prospective Fathers.*

By Mario A. Castallo and Audrey Walz. The Macmillan Company, New York. $1.75. xiii + 110 pp. 1943.

Long before the printed word, books were written to give insight and advice to the layman in regard to pregnancy and parturition. The great first century A.D. Greek text of Soranus on obstetrics and gynecology was apparently written for physician, midwife, and literate layman alike. When medicine was so little a specialized science, the educated layman had little or no difficulty in translating the verbiage or the thought processes of medicine into his own intelligence. This is not true of modern medical science, for it is explained in terms and disciplines that are only intelligible to the fully initiated, and often to them only with the aid of a trade dictionary. This is not stated as a criticism but as a fact. The obvious result is the recent publication of a whole library of popular books on various matters medical. The largest shelf of this library is given over to insight and advice books on the stork and his exciting avocation. Certainly this is natural enough, for no major medical phenomenon affects so many people so often.

Castallo, Assistant Professor of Obstetrics at Jefferson Medical College, and Gynecologist to St. Agnes and to St. Mary's Hospital, is the latest author to try his skill at popularizing medicine. The resultant book, *Expectantly Yours*, is a highly creditable performance both in its contents and form. It is illustrated with excellent pen and ink sketches by Helen G. Schad.

In the opening chapter the author allays the fears of his readers by stressing the current low mortality figures, which would even be "a third lower" if immoral abortions were not included. He further points out to his readers that those who do not read such books, "the underprivileged one-third of a nation who eat too little and work too long and hard," contribute more than their third to the death toll. Castallo could have contrasted the mortality figures of the white and colored groups to make this point even sharper, but he did not.

In the seven brief pages of Chapter Two, "The Facts of Life," the author reveals the bare essentials of conception, sex-ratio, and maternal impression. Next follows a discussion of the initial visit to the obstetrician, and the training rules he lays down. In "Mind over Matter" the author tries to argue the pregnant woman out of hypersensitivity to her anterior bulge. In his eyes she simply exchanges her non-pregnant glamour for a spiritual beauty; she metamorphoses from a Varga Esquire girl to the central figure of Botticelli's "Spring." In too "polyannish" a vein he glosses over the chances for abnormal offspring. The book suffers from a lack of frankness about the unpleasant, which I think would intellectually insult me were I the lay reader. The fact that I am not the ordinary pregnant reader and can never be, makes the latter statement of uncertain value.

Thirty pages are devoted to labor and delivery. Such practical details as to what to take to the hospital for mother and baby are included, as well as a discussion of spontaneous birth, forceps delivery, and Cesarean section. The matter of pain relief in labor is discussed in relative detail. Fifteen pages are devoted to the puerperium (the "come-back period"). Exercises to strengthen the abdominal musces are well depicted in line drawings with appropriate descriptions beneath. The emotional redjustment to include another loved one beside the husband, and its sexual sequelae are treated very sympathetically. The concluding chapter is concerned with the technique of infant care: feeding, diapering, and bathing.

Castallo's book is authoritative and accurate. It is written in an informal, almost breezy style, always addressing the reader with the personal pronoun "you." The facts are presented in a naked, pleasant, and concise form, with few historical, literary, or statistical trimmings. I think it is ideal for the unsophisticated reader, but I doubt whether a college major in biology would find it intellectually satisfying in the quest for knowledge of her pregnant self.

Alan F. Guttmacher

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ANIMAL MORPHOLOGY

Anatomy *As a Basis for Medical and Dental Practice. By Donald Mainland. Paul B. Hoeber Inc., New York and London.* $7.50. xvii + 863 pp. 1945.

This new textbook of human anatomy is both unusual and interesting, neither of which adjectives can be applied to many texts of gross anatomy. Three underlying tenets appear in the writing of this book: first, the definition and interpretation of anatomical structures in view of their function; second, the organization of such data into topographical and physiological systems; and third, the presentation of facts in a manner to encourage the student to *think* Anatomy rather than to memorize it.

There are two main parts of the book. The first and shorter part (152 pages) is a general, correlative discussion of the systems of the body. Mainland has taken pains to point out repeatedly that gross anatomy is not a dogmatic or a static science. He has done this by placing considerable emphasis on the omnipresence of variation, both human and comparative, and on the relation of structure and function. The author's method of argument is well illustrated by his discussion (pp. 80–84) of the factors, influencing the inner structure of bones, especially the formation of trabeculae as formulated by Wolff. The criticism of the Wolff doctrine brings sharply to the reader's mind that the factors regulating bone structure are diverse, variable, and not by any means fully understood.

The second section of the text (586 pages) is topographic in organization, but the same insistent questioning tends away from a cut-and-dried presentation. The text throughout is sprinkled with references to the literature, and the length of the bibliography (33 pages) indicates a broad coverage of the field. This contrasts with the last edition of one of the standard textbooks of anatomy, which contains only 149 references to the literature, which, if gathered together, might amount to 5 pages, and among which the most recent paper appended to the chapter on the skeletal system was written in 1923!

In attempting to evaluate this new text, it must be borne in mind that it is to be used in conjunction with an atlas, and probably with a standard text as a reference. The book is a radical departure from the usual approach, and consequently will not be welcomed by those who abhor any change in method. It seems that in the attempt to simplify and condense, the author has catalogued the material in a manner which makes for choppy reading. The dynamic, *biological* approach, however, will not only make the subject interesting to the student, but will enable him to evaluate from the anatomical side the reversible equation of structure and function. In such an understanding lies the future of anatomy, both for the surgeon and practitioner, and for the research worker.

James M. Sprague

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Structure and Function as Seen in the Foot. *By Frederic Wood Jones. William Wood, Williams and Wilkins Company, Baltimore.* $7.50. iv + 329 pp. 1944.

This volume does not possess the stimulating originality of the previous books by Frederic Wood Jones (*Arboreal Man*, 1916; *The Principles of Anatomy as Seen in the Hand*, 1920 and 1942; *Man's Place among the Mammals*, 1929), but it is a useful, detailed compilation of facts, describing the macroscopic anatomy of the foot of man, with special reference to function. For an anatomical treatise it is unusually lively and readable, partly because it includes many topics not to be found in standard textbooks of human anatomy. Thus, there are chapters dealing with the principles of terminology, the human foot in phylogeny and in ontogeny, the digital formula, the metatarsal formula, and external characters, such as flexure lines, cleavage lines, papillary ridges, and hair, but not a word on nails. The largest part of the book is devoted to the discussion of bones and muscles (195 pages), nerves and blood vessels receiving less attention (58 pages). The treatment of these subjects gains a great deal by frequent references to individual variations, age changes, racial differences, etc., which are all too often neglected in our textbooks.

Throughout this work the author attempts to support his pet hypothesis that "in the anatomy of the human foot there is abundant evidence that it is derived from a primitive mammalian foot, retaining its primitiveness probably because of the arboreal habit. Such a foot we have every reason to believe belonged to the primitive members of the Primate stem—the stem from which Man and the other existing members of the

Primates branched apart and went their separate way at a very early stage in the Primate story." In pleading his case the author conveniently ignores many observations, recorded in recent literature, which constitute good evidence against his untenable claim.

The "References for Further Reading," appended to each chapter, include many titles of historical interest, but they omit a considerable number of significant contributions of the last two decades. The one hundred and fifty somewhat crude and diagrammatic illustrations could have been greatly improved with little trouble by a competent illustrator.

In spite of its shortcomings (and its high price) the book as a whole forms a welcome and useful addition to the literature of human anatomy.

A. H. SCHULTZ

THE PRECENTRAL MOTOR CORTEX.

Illinois Monographs in the Medical Sciences, Volume IV, Nos. 1–4. Edited by Paul C Bucy. The University of Illinois Press, Urbana. $5 50 (cloth); $4.50 (paper). xiv + 605 pp. 1944

Exactly seventy-five years have elapsed since Fritsch and Hitzig first demonstrated the existence of an excitable motor area by directly stimulating the cerebral cortex of mammals. Since that time, largely by virtue of the techniques of stimulation and ablation, and more recently by action potentials, a great mass of data has been collected and synthesized. This volume, under the editorship of Paul Bucy, presents the current status of our knowledge of the cerebral motor cortex. It serves not only to bring together the scattered observations in convenient form, but also to indicate the gaps in existing knowledge and the more likely directions of future research. The seventeen original chapters have been written by fourteen authors, all of whom have made major contributions to one or more aspects of the subject. John F. Fulton has written a "Foreword."

Bucy, in his "Introduction," defines the precentral motor cortex as "the principal efferent or effector cerebral cortical mechanism by which the brain expresses its activity through the skeletal musculature. The portion of the precentral region principally so engaged is the cytoarchitectonic areas 4, 6, and 44."

Gerhardt von Bonin discusses the "Architecture of the Precentral Motor Cortex and Some Adjacent Areas." This includes many new, hitherto unpublished observations. Noteworthy among his conclusions are recognition of a layer IV in the precentral agranular cortex and the identification of an area 44 (Broca's area) in all of the non-human primates which he has studied (*Galago*, *Cebus*, *Macaca*, chimpanzee). It formerly had been thought, on the basis of Brodmann's work, that this area was peculiar to man. Brodmann regarded this region as belonging to area 6 in other primates. If von Bonin's interpretation is substantiated, then a "speech area" is common to primates in general and so distinguishes them from other mammals.

James L. O'Leary deals with "The Role of Architectonics in Deciphering the Electrical Activity of the Cortex." "Afferent Connections" are treated by A. Earl Walker; "Efferent Connections" by Paul M. Levin; "The Pyramidal Tract" by Sarah S. Tower; "Cortico-cortical Connections" by Warren S. McCulloch; "Somatic Functions" and "Autonomic Functions" by Margaret A. Kennard; "Relationship to the Cerebellum" by Percival Bailey; "The Frontal Eye Fields" by Wilbur K. Smith—the latter, although not included in the term precentral motor cortex, since they occupy area 8, are considered here because they are concerned with the innervation of striated muscle and also function as a suppressor area having many of the characteristics of area 4s. "Electrical Excitability in Man" is discussed by Theodore C. Erickson; "Effects of Extirpation in Man" and "Relation to Abnormal Involuntary Movements" by Bucy; "Clinical Symptomatology" by Charles D. Aring; "Pathology" by Charles Davison; and "Significance of the Precentral Motor Cortex," an appraisal of the results of stimulation and ablation, by Marion Hines. Respecting the question whether the representation in the motor cortex is of individual muscles or of movements, Hines points out that the two views are not incompatible. Chapter VII is a translation by von Bonin and McCulloch of Bubnoff and Heidenhain's old but significant paper, "Ueber Erregungs- und Hemmungsvorgange innerhalb der motorischen Hirncentren" (Arch. ges. Physiol., 1881, 26. 137–200). There is a bibliography of 797 titles.

One is impressed, after going through this splendid volume, by how little of our existing knowledge of the precentral motor cortex has been secured from direct observations of man. This, of course, might be expected in view of the many difficulties involved. The chief source of recent knowledge has been the rhesus monkey, and, in considerably less degree, the chimpanzee. One of the urgent problems is how to secure more and better data for man. All catarrhine primates no doubt agree in many fundamental details, but it scarcely need be stressed that striking species differences are to be expected.

W. L. STRAUS, JR.

ATLAS OF THE BLOOD IN CHILDREN.

By Kenneth D. Blackfan, Louis K. Diamond, and C. Merrill Leister (illustrations). The Commonwealth Fund, New York. $12.00. xiv + 320 pp., including 70 colored plates. 1944.

In his foreword, George N. Minot points out the great need for pictures of the blood of children, for, as he notes, the blood of the child shows a much greater variability than does that of the adult. "Lability of children's blood is the rule. . .and the younger the individual the greater the instability." This tends to make diagnosis or evaluation of the blood picture in the child more difficult than in the adult. Furthermore, the same stimuli may produce quite different blood pictures at the two stages of life.

This handsome volume, subsidized by the Commonwealth Fund, more than satisfies this need. It is based upon observations on more than 5,000 infants and children (many followed for several years) recorded by the late Dr. Blackfan and by Diamond over a period of many years. The text (144 pages) comprises useful, brief accounts of the various blood diseases—etiology, symptoms, laboratory picture, course, prognosis, and treatment. Case histories are included. It is divided into 5 chapters: (I) Blood Cells—a good introductory account of normal blood cells, their life history, and hemopoiesis; (II) The Erythrocytes in Anemia (the normocytic normochromic anemias, the macrocytic hyperchromic anemias, the microcytic hyperchromic anemias, the anemias associated with jaundice); (III) The Leukocytes in Disease (leukocytosis and leukopenia, neutrophilic leukocytosis, neutropenia, eosinophilic leukocytosis or eosinophilia, lymphocytosis and lymphopenia, monocytosis); (IV) Leukemia; (V) The Platelets (thrombocytopenia, thrombocytosis and thrombocythemia). A bibliography of 14 pages is appended.

The chief glory of the volume are the superb drawings of Wright's stain preparations of normal and diseased blood by Leister, who represents the rare combination of pediatrician and artist. These are beautifully reproduced as 70 lithographic plates in eight colors, with excellent accompanying keys and legends.

This atlas will recommend itself not only to pediatricians, but to others—such as general medical men, hematologists, pathologists, and anatomists—as well. For there really is nothing like it, and its usefulness extends well beyond the relatively narrow implications of its title.

As a sort of a castle in Spain, may one be permitted to wonder if the utility of such a work would not be enhanced for one of its avowed purposes—to assist medical students and physicians in the identification of cells in blood diseases—if illustrations of mediocre blood films had also been included? This may sound like heresy, and malapertness toward Leister and his fine illustrations. But these indeed have been taken from exceptionally fine films. Anyone who has tried to prepare blood with Wright's or similar stains knows that it is not the lot of other than the expert or near expert to attain such excellence; hence it is the ordinary, mediocre preparation that most frequently will require interpretation.

W. L. STRAUS, JR.

ANIMAL PHYSIOLOGY

ANNUAL REVIEW OF PHYSIOLOGY. *Volume VII. 1945.*

Edited by James Murray Luck and Victor E. Hall. The American Physiological Society and Annual Reviews, Inc., Stanford University P. O. $5.00. viii + 774 pp. 1945.

This annually published volume of reviews has become indispensable to the physiologist and has been welcomed by the personnel of other branches of biological science. The volume published in 1945 contains twenty-six articles, which cover the literature published in these fields during the last three to five years. Subjects reviewed are permeability, the physical properties of protoplasm, the physiological effects of radiant energy, physiological aspects of genetics, developmental physiology, water metabolism, physiological effects of heat and cold, energy metabolism, the peripheral circulation, respiration, muscle, digestive system, kidney, blood, the lymphatic system, heart, electrical activity of the brain, conduction and synaptic transmission in the nervous system, the somatic functions of the nervous system, the special senses, metabolic functions of the endocrine system, hormones in reproduction, exercise, physiological psychology, applied physiology and pharmacology. These reviews vary enormously in scope and type. A few of the reviewers because of the more specific and limited nature of their topics, were able to give an analysis of the present state of knowledge of certain functions. In the majority of cases, however, the fields to be covered were so large that the reviewers could do little more than list and classify recent contributions. The chief value of this volume resides in the fact that it will be of great assistance to those who wish to keep informed concerning a massive and varied literature. The contributors, for the most part, have justified the assumption that in their summaries they would not fail to describe all pertinent articles of recent date.

CHANDLER MCC. BROOKS

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PHYSIOLOGY IN HEALTH AND DISEASE. *Fourth Edition, thoroughly revised.*

By Carl J. Wiggers. Lea and Febiger, Philadelphia. $10.00. 1174 pp. 1944.

This is the fourth edition of one of the advanced modern textbooks of physiology. The author has attained a high degree of success in his effort to bring various discussions into accord with the physiological thinking of the day. On reading this book one is constantly impressed by the author's ability to summarize and present the mass of information now available in the numerous and diverse fields which students of physiology must consider. The topics covered in the nine sections of this book are: (1) muscular contraction and associated phenomena; (2) the physiology of the peripheral and central nervous systems; (3) the blood; (4) respiration; (5) the heart and circulation; (6) physiology of the alimentary tract; (7) metabolism and nutrition; (8) excretion and body fluids; and (9) the endocrine organs. Decisions reached in discussions of controversial subjects are frequently different from those described in other textbooks of like scope, but references are given which permit the reader to find the available evidence and to form his own opinion if he so desires. Each subdivision of the major sections of the book contains an explanation of some physiological mechanism, and this is generally supplemented by a brief summary of the abnormalities of function consequent to various pathological processes. The sections which deal with the mechanism of the function of the cardiovascular system are very well conceived and clearly written. Those textbooks in which the various sections have been contributed by men who have specialized in those particular fields convey a somewhat higher degree of authority and attain a greater completeness of presentation, but they generally sacrifice uniformity of performance and clarity, qualities which this textbook possesses.

Chandler McC. Brooks

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Laboratory Manual for Elementary Physiology. *Fourth Edition.*

By Lalia V. Walling and Kenneth Siler. The C. V. Mosby Company, St. Louis. $1.50 (paper) 187 pp. 1945.

This laboratory manual contains 116 exercises which may be performed with simple equipment by students who have had little previous training in the biological sciences. The thirteen major topics treated are: the physiology of muscle and nerve, the central nervous system, sense organs, the circulation, blood, respiration, and the digestive system. Considerations of chemical tests for foods, metabolism, heat regulation, and excretion are likewise included. The procedures outlined are much too elementary for advanced students but may be suitable for college courses in physiology. The number of exercises seems to be rather excessive, and one wonders whether it would be possible or, for that matter, of value to the students to perform all of them. If properly supplemented with correlated lectures, such a laboratory course as is outlined in this manual would aid in giving students a good though elementary knowledge of certain body functions.

Chandler McC. Brooks

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Laboratory Notes in Physioloy. *Second Edition.*

Compiled by William R. Amberson, Dietrich C. Smith, Robert H. Oster, Robert S. Anderson, Joye J. Jennings, and Mary E. Chinn. The Williams & Wilkins Company, Baltimore. $2.25. iv + 91 pp. 1944.

This brief laboratory manual contains descriptions of twenty-nine experiments, which have been classified under five headings. The experiments of section I deal with muscle and nerve, those of section II with the central nervous system and the special senses. Section III contains a series of mammalian experiments that include studies of the cardiovascular system, respiration, and the secretion of saliva, bile, and pancreatic juice. Sections IV and V deal with respiration, metabolism, circulation, and water balance in man. All of these experiments are of value, they involve procedures which are not too complicated for successful performance by the average medical student, and the results which are sure to be obtained are highly instructive. No more need be said than that this is a well conceived and well written guide which could be employed in any laboratory engaged in the teaching of physiology to advanced students.

Chandler McC. Brooks

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Your Digestive System.

By Louis Winfield Kohn. The New Home Library, The Blakiston Company, Philadelphia. 69 cents. xiii + 274 pp. 1944.

The primary purpose of the author of this book is to acquaint the common reader with the various factors involved in the production of digestive disorders, and to help him note the many symptoms which indicate the need for medical attention. Consequently, a brief introductory summary of the anatomy and function of the digestive tract is followed by a series of chapters which describe the diseases of this system. Information is given concerning the diagnosis, nature, and consequences of the diseases which commonly occur in various portions of the gastro-intestinal tract. Descriptions are sufficiently simple and clear to permit the common reader to greatly increase his knowledge of this important system of organs and the symptoms of their pathology. It is hoped, however, that reliance on books of this type will cause no one to question the advisability of seeking periodic examinations by a qualified physician. The absurdly diagrammatic illustrations detract from the respectability of this publication. For example, no value can be attached to illustrations which locate the liver, gall bladder, pancreas and stomach within the thorax (pp. 28, 110, 136, 201, etc.).

Chandler McC. Brooks

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Your Respiratory System.

By Herman Pomeranz. The New Home Library, The Blakiston Company, Philadelphia. 69 cents. xvii + 298 pp. 1944.

This book is intended to contain basic information of a scientific nature, so presented as to be readily understood by the general reader. The author's stated aim was to include in one volume a non-technical description of the respiratory system, its structure, functions, diseases, treatment, and hygiene. These aims have been partially attained; the book does contain a thorough and simple description of the anatomy and pathology of the respiratory organs. However, comparatively little is said concerning the control and function of these structures. A large proportion of the volume is devoted to a description of diseases of the lung, early symptoms, diagnostic methods, and treatment. Since the emphasis of the entire work is on pathology, the chief value of the book probably lies in the fact that it does contain easily understood descriptions of the consequences of abnormalities of various structures of the system and descriptions of the signs of developing pathology. The reader consequently might be more intelligent in his decision as to when he should seek the aid of a physician. In addition, the book has some value as a reference work, but one may doubt whether the general reader will be sufficiently interested in the subject matter to voluntarily read it completely. Facts are accurately stated for the most part, but there are a few errors, such as the statement that "an intrapulmonic air pressure of over 60 millimeters of mercury will cause a separation of the pleura from the lung and result in an air bubble." The intrapulmonic pressure normally varies between a few millimeters below and above 760 millimeters of mercury and when one forcibly expires, pressures may rise to 860 millimeters (100 mm. above atmospheric) without damage to the lung. One also tends to question the statement that a given area of nasal mucous membrane gives off seven times as much carbon dioxide as a similar area of alveolar wall, but the book gives no clue as to the sources of the author's information. In summary, it can be said that the book is acceptable, and that the reviewer enjoyed reading it and learned numerous things during this study.

Chandler McC. Brooks

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Manometric Techniques and Related Methods for the Study of Tissue Metabolism.

By W. W. Umbreit, R. H. Burris, and J. F. Stauffer. Burgess Publishing Company, Minneapolis. $3.50 (paper). iii + 198 pp. 1945.

This manual is a compilation of techniques which are commonly used in the study of tissue metabolism. As described, they are adequate for studies undertaken by graduate students working under the direction of a mature investigator. Experienced workers will welcome this manual as a handbook to aid them in broadening and improving certain of their technical procedures.

The authors have attained their declared aim in describing methods which have been well tested and are commonly employed, which require a minimum of equipment and only that equipment available in biological laboratories and which, though not describing manometric measurements, are essential to the study of tissue metabolism. The topics dealt with in the sixteen chapters of the book will give one a clear idea of the great value of this manual to those who are interested in obtaining knowledge of the metabolic processes of individual tissues. The chapter titles are: (1) the Warburg constant volume respirometer; (2) the "direct method" for carbon dioxide; (3) carbon dioxide and bicarbonate; (4) the "indirect" method of Warburg; (5) useful techniques for use with manometric methods; (6) determination and use of flask constants; (7) the differential manometer with special reference to its use in studies of photosynthesis; (8) methods of tissue preparation; (9) the homogenate technique; (10) chemical methods; (11) special methods employing manometric techniques; (12) "Thunberg" techniques for estimation of dehydrogenase activity; (13) related electrometric techniques; (14) manometric estimation of metabolites and enzyme systems; (15) methods for the analysis of phosphorylated intermediates; (16) preparation of physiologically important intermediates and metabolites. This book is recommended to all those interested in this aspect of physiological investigation.

Chandler McC. Brooks

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Die Hormone: *Ihre Physiologie und Pharmakologie. Erster Band: Keimdrusen, Hypophyse, Nebennieren. Zweiter Band: Schilddruse, Nebenschilddrüsen, Inselzellender Bauchspeicheldruse, Thymus, Epiphyse.*

By Paul Trendelenburg. Volume 2 edited by Otto Krayer. (Julius Springer, Berlin); J. W. Edwards, Ann Arbor, Michigan. $9.00 (vol. 1); $11.50 (Vol. 2). xi + 351 pp. (vol. 1); x + 502 pp. (vol. 2). (1929; 1934); 1944.

The first volume of Trendelenburg's *Die Hormone* originally appeared in 1929 with chapters on the gonads, the pituitary, and the adrenal glands; the second volume, dealing with the thyroid and parathyroid, pancreas, thymus, and pineal glands appeared in 1933, postdating the death of the author in 1931. Both volumes have now been reprinted by the Alien Property Custodian. Each chapter in these volumes is monographic in scope, and both the older literature and that to date of publication are covered with considerable thoroughness. It may not be amiss, then, to consider these volumes briefly in the light of developments that have occurred subsequently to their first appearance.

Volume I in particular demarcates a break between old and new trends. It was published in the same year that the isolation of the female sex hormone by Doisy and by Butenandt opened up the field of the steroid hormones to the pure chemist, and, for the biologist, replaced crude organ extracts by known chemical entities. Meanwhile, emphasis shifted from adrenal medulla to adrenal cortex, and from the posterior pituitary to the anterior lobe. The extension of pituitary control to metabolic processes postdates Trendelenburg's chapter on the pituitary gland; however, the early work of Houssay that initiated this development is dealt with in some detail in the chapter on the pancreas. Those portions of Volume I, considerable in scope, dealing with the pharmacological properties of posterior pituitary extracts, and of extracts of the adrenal medulla, and adrenalin, together with large portions of Volume II, seem less dated by the passage of a decade. The thymus and the pineal body are with us still, obscure and not a little obfuscated. The hormone of the pancreas, produced in immense amounts annually, yields its secrets reluctantly, and advances in pancreas physiology have largely concerned its interrelationships with the pituitary and adrenal glands. The parathyroid hormone has proven refractory. In the thyroid field, the main advances to be recorded are the application of radioactive tracers to the kinetics of iodine uptake, and of histochemical techniques and microdissection to the study of colloid deposition and removal. Recently the effects of the pure chemical substances, thiouracil and alloxan, on thyroid and pancreas hormone secretion, respectively, have been exploited as techniques for the study of these hormonal mechanisms. The decade has witnessed some real progress in the isolation and definition of protein hormones of the anterior pituitary body, and of the pituitary-like substances of blood and urine.

These volumes of Trendelenburg contain much material of permanent value to the endocrinologist and pharmacologist, besides forming useful markers along the line of progress. They can be recommended as systematic introductions to the subjects considered, and for their coverage of literature that does not neglect the historical contributions in the various fields.

H. R. CATCHPOLE

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THE MALE HORMONE.

By Paul de Kruif. Harcourt, Brace and Company, New York. $2.50. 243 pp. 1945.

This is the tenth of Paul de Kruif's books in the field of popular medical science. In it he succeeds again in dramatizing apparently dull facts and in presenting them understandingly to the general reader. Unfortunately, the book is less successful than the others, notably *The Microbe Hunters.* De Kruif has here, as often before, overdramatized because of his own self-admitted enthusiasm, doubtless accentuated in this instance by his personal experience with the beneficial effects of the drug he is discussing. Over-enthusiasm has often been dangerous in endocrinology because of the great gap between the more extravagant claims for the hormones and their actual benefits in therapy. Generally, however, De Kruif has managed to temper his enthusiasm with warnings as to some of the limitations of hormone treatment.

Can it be that testosterone is responsible for the somewhat lusty and ribald flavor of this book, and its vocabulary involving slang from the street and the laboratory? The combination has produced an unfortunate tone of vulgarity that vitiates De Kruif's purpose of presenting the case for testosterone without reticence and without prudery.

The author has used his book as a platform on which to air some of his prejudices. Many pages are devoted to a eulogy of Dr. Herman Bundesen of Chicago, whose chief claim to mention here is that it was he who first persuaded De Kruif to take testosterone. Throughout the book much space is devoted to presenting the investigators as the shining knights of medicine and the practitioners, particularly the specialists, as the black dragons who have killed progress and are more interested in death than in life. This sort of thing succeeds more in irritating than in being constructive. Sir William Osler, for instance, whose teachings have inspired so many to contend against death with skill and courage, is charged with a generally defeatist attitude toward serious disease and with being responsible for stamping "a mood of resignation against death upon modern medicine." Such prejudices serve to obscure the soundness of De Kruif's basic criticisms.

The Male Hormone, however, remains an exciting account of the search for testosterone and its development into a valuable therapeutic agent. Once more De Kruif has demonostrated his ability to vivify for the general public the selfless and often undramatic devotion of the investigator.

GEORGE W. CORNER, JR.

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ELECTROENCEPHALOGRAMS OF NORMAL CHILDREN. *Monographs of the Society for Research in Child Development, Volume IX, No. 3. Serial No. 39.*

By Charles E. Henry. Society for Research in Child Development, National Research Council, Washington. $1.50 (paper). xi + 71 pp. 1944.

This is the third in a series of reports of the Brush Foundation study of the growth and development of normal children. It is based on a study of almost 4,000 electroencephalograph records, many of which represent successive examinations of the same individuals over a period of years.

The aims of this study were to establish electroencephalographic standards, to explore the possible correlations between EEG variables and other measurements of physical and mental development, and to determine the incidence of normal and questionably normal EEGs in a large group of presumably normal children.

It was found that there may be considerable variability in the form of individual growth curves. Some evidence of sex differences was secured. Attempts at correlations of alpha frequency and percent-time-delta with IQ and skeletal maturity were not significant. The incidence of abnormal records in this supposedly normal sample is discussed.

HEALTH AND DISEASE

Familial Susceptibility to Tuberculosis: *Its Importance as a Public Health Problem. Harvard University Monograph in Medicine and Public Health Number 5.*

By Ruth Rice Puffer. Harvard University Press, Cambridge, Mass. $2.00. x + 106 pp. 1944.

Although its mode of inheritance still remains to be worked out, the existence of a genetic basis of susceptibility to tuberculosis may be regarded as fully established by the studies of Kallmann and Reisner on the differences in the incidence of the disease in monozygotic and dizygotic twins, siblings, and parents, and by the extensive study of tuberculosis in Williamson County, Tennessee, which takes the central place in this monograph. The author uses, throughout, the ambiguous term "familial susceptibility" favored by the medical fraternity, but it is clear from context and data that nearly if not always it is genetic susceptibility that is meant, and not a common susceptibility due to shared familial environment.

The subject is introduced by a historical survey of the problem and a discussion of "familial" susceptibility in leprosy, rheumatic fever, poliomyelitis, and diabetes for comparative purposes, as well as of experimental tuberculosis susceptibility in guinea pig and rabbit strains. The four principal chapters deal with tuberculosis in siblings, in consorts, in parents, and in children of index cases. These summarize a great deal of interesting statistics. In the Williamson County study, death rates of siblings of index cases are higher than those of siblings of consorts of the index cases, the latter group serving as controls. Most siblings were adult and separated, so that this difference shows the effect of common heredity. Tuberculosis in consorts of active (sputum-positive) cases was higher than in those of sputum-negative cases. Manifest tuberculosis was found to be higher when the consort comes from a family with parental or sibling tuberculosis than when the consort comes from a non-tuberculous family (33.3% against 11.1%). It is especially important, if confirmed, that the death rate from tuberculosis of consorts is *less* than that of siblings of the index cases, in spite of the factor of current exposure in the consorts and of separation in the siblings. The data on tuberculosis in parents and children of index cases offer further confirmation of the importance of the genetic factor.

In one respect the treatment of the data in the discussion seems faulty. Measures of the significance of differences in the comparisons made are not given. In many cases the partition of the individuals into groups makes the numbers in the groups compared rather few, and there is little doubt that some of the comparisons, made between percentages, do not possess statistical significance. In a few places, recognition of this is evident, and once or twice the author refers to the calculation of a Standard Error. In the great majority of instances, however, the reader is left to his own conjectures or calculations. The difference, mentioned above, between the consorts from tuberculous and non-tuberculous families is, for example, of doubtful statistical significance ($P = .02 - 05$). This methodological flaw considerably detracts from the merit of an otherwise fine piece of work.

In conclusion, the author applies her findings to the control of tuberculosis. She lays special emphasis on the value of searching for cases among siblings, parents, and children of persons known to have tuberculosis, irrespective of their present household. Past emphasis upon household exposure to tubercle bacilli has not been very effective in helping to locate fresh cases, although of course household associates of cases should continue to be examined as a matter of precaution. If these policies can be put generally into practice, we may expect a much higher proportion of early diagnoses, with all that that promises for eventual victory over one of man's most stubborn foes.

Bentley Glass

A Textbook of Pathology: *Pathologic Anatomy in Its Relation to the Causes, Pathogenesis, and Clinical Manifestations of Disease.*

By Robert Allan Moore. W. B. Saunders Company, Philadelphia and London. $10.00. xii + 1338 pp. 1944.

This tremendous volume contains a summary of almost every pathological condition listed in the Quarterly Cumulative Index Medicus. In this respect, it forms a complete catalogue of disease, and can be recommended as a reference book for the advanced student.

As a textbook of pathology, however, its very length and comprehensiveness serve as handicaps. Facts are given on so many unimportant subjects that important ones fail to be properly emphasized.

The format departs somewhat from the conventional method of presentation. The section on general pathology includes all diseases of known etiology and is further subdivided into metabolic diseases, inflammations, and tumors. Diseases of unknown or obscure causes are described in the section on special pathology, under the organ in which they occur. As a reference book, therefore, there is no difficulty in locating desired information. As a textbook, however, the sequence of subjects will be rather complicated and difficult for the medical student to follow. Brief definitions of types of inflammation are given in a preliminary survey of this subject, but more comprehensive descriptions of infections are made according to portals of entry. Thus, many complicated diseases must be studied before the simpler pyogenic infections are completed; and there is no comprehensive view of many agents of disease with multiple portals of entry.

The volume is illustrated profusely. Many of the illustrations are excellent and serve not only as illustrations of pathological processes, but aid in the correlation of the pathological material with clinical observations. Illustrations of spontaneous and experimental diseases in lower animals are interesting; and charts and diagrams of the distribution of diseases and of other statistical data are especially helpful. It seems unfortunate, therefore, that with so much original material available for illustrations of pathological processes, large numbers of reprints from previously published material has been used. For instance, at least sixteen illustrations were reprinted from MacCallum's *Textbook of Pathology* alone.

The bibliography is voluminous. References are listed according to subjects and are further explained by complete titles. This is a distinct service to readers seeking specific information.

To reiterate, this volume will aid the student interested in rare and obscure diseases, and will serve as a helpful reference volume rather than as a conventional textbook of pathology.

Ella H. Oppenheimer

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Health and First Aid.

By Morris Fishbein and Leslie W. Irwin. Lyons and Carnahan, New York. $1.20. vi + 372 pp. 1944.

In Part I of this carefully prepared little volume, the authors have presented, in clear and non-technical fashion, an abundance of pertinent, scientifically accurate facts relating to personal hygiene in the preservation of health and the prevention of disease. Special emphasis is placed upon the most reliable methods of preventing the spread of common diseases, and in the most acceptable practices in caring for the body in everyday living. Such topics as sleep, fresh air, exercise, posture, fatigue, bathing, clothing, and diet, as related to the maintenance of good health, are discussed with authority and completeness. An excellent chapter has been included on the effects of alcohol and tobacco on the body. The methods and materials of first aid, and the important aspects of accident prevention have been presented in Part II of the volume. The latest methods (derived from the medical experience of the present war) for the treatment of shock and serious wounds have been thoroughly discussed. Each chapter is provided with a series of questions designed to test the reader's understanding of the material covered in that chapter. The work will serve well as a text-book for high school courses in hygiene or as a home reference book.

B. Aubrey Schneider

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Contagious Diseases. *A Guide for Parents. Second Edition.*

By W. W. Bauer. Alfred A. Knopf, New York. $2.50. ix + 188 + iv pp. 1944.

In an authoritative, not to say authoritarian, manner, the author discusses for the layman—in particular, for mothers—what they should know about quarantine, home nursing, and the various contagious diseases their children are likely to contract. The complications of home nursing, as outlined, will probably terrify most mothers into insisting on hospitalization for everything. On the other hand, the author is clear and forthright as to the need for quarantine and the character it should assume in varying circumstances. The chapters on the individual diseases are excellent. Unnecessary fears are allayed; methods of prevention, if available, are described; symptoms and appropriate care are given in sufficient detail; and of course we are told in every case not to attempt home medication, but to call the doctor. The omission of Rocky Mountain spotted fever (tick fever, as it is generally called, at least in this area) is a bit surprising, since it is becoming commoner yearly, and mothers certainly show more concern about it than about some of the diseases that are included. All in all, however, this is a very instructive and useful handbook for the home, and its standard is high. It should also be useful in courses of hygiene.

Bentley Glass

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The Common Cold *and How to Fight It.*

By Noah D. Fabricant. Ziff-Davis Publishing Company, Chicago and New York. $1.50. 107 pp. 1945.

Whatever can be said today about colds, plain and fancy, is said here in accurate, simple, and entertaining fashion. The author, an ear, nose, and throat specialist, discusses the respective merits of nose drops, vitamins, vaccines, alkalinizing, and sulfa drugs, and cautiously explores the possibilities of future research for overcoming this most frequent enemy of good health. He fares afield into allergy and sinus and mastoid complications sufficiently to show their relations to the common cold. This brief volume must be rated high among popular presentations of medical subjects.

THE WOMAN ASKS THE DOCTOR.

By Emil Novak. The Williams & Wilkins Company, Baltimore. $1.50. ix + 130 pp. 1944.

In this slender book, a gynecologist has undertaken to answer in simple language the common questions women ask him. He has succeeded very well indeed. He includes a simple account of sex determination and of sex differentiation—in the former, he makes the error of attributing it to the potency of the Y chromosome. His chapter on the superstitition and folklore of menstruation is amusing and good medical history. The anatomy of the reproductive organs, the nature and significance of menstruation, the role of the endocrine glands, puberty, menopause, disorders of menstruation, causes of sterility, and cancer of reproductive organs or of the breast form the natural divisions of his subject. He concludes with a brief chapter on the sex life of women and on methods of contraception, in which he gives a qualified recommendation of the Ogino-Kraus "safe-period" theory. The standard of factual accuracy is high and the discussion clear. Women will find it most valuable, both for personal reference and as a help in the sex education of their daughters. It should be very useful as reading or text material in courses of hygiene for girls up through the elementary college level.

A NATIONAL HEALTH SERVICE *Presented by the Minister of Health and the Secretary of State for Scotland to Parliament by Command of His Majesty February 1944.*

Ministry of Health, Department of Health for Scotland. The Macmillan Company, New York. 75 cents (paper). 85 pp. 1944.

Any plan for complete national social security must, of necessity, include a comprehensive public health organization capable of rendering, free of charge, to each and every citizen of the nation, irrespective of economic status, age, sex, religion, or political affiliation, such medical care and advice as may be necessary for the maintenance of a healthy population and a high standard of living. The organization must provide, in addition to the present services of care for the insane, the quarantine and treatment of certain communicable diseases, school and home nursing, etc., every form of health care from the general treatment of diseases and disabilities in the home, to the more specialized branches of medicine and surgery obtainable only in the hospital or sanatorium. The structure and activities of just such an organization are presented in this report by the Minister of Health and the Secretary of State for Scotland.

The system herein outlined for Britain does not completely replace the present system of public health, but is organized around the firm foundations of the existing system. The organization provides sufficient flexibility for the incorporation of a wide variety of existing local health organizations and circumstances, and has attempted to reconcile the two extreme points of view regarding health care, i.e., individual medical care, and completely socialized medicine. A large share of the responsibility of instituting such a system will fall upon the shoulders of the central and local medical advisory boards, whose recommendations to the central or local health officers will be based on existing conditions and the needs of the population at the moment. The service will be financed partly by central and partly by local funds, to which will be added the contributions of some sort of social insurance.

Detailed discussions of (a) the existing health service of Britain, (b) earlier proposals for improving the service, (c) methods of administration of the service, (d) the remuneraion of general practitioners, and (e) the financing of the system, are appended.

B. AUBREY SCHNEIDER

FOOTE'S STATE BOARD QUESTIONS AND ANSWERS FOR NURSES. *Essay and Objective Types Compiled from Actual Examination Questions Given Throughout the Country by State Examining Boards. Twenty-third Edition, Revised.*

By Jimmie K. Bratton et al. (Editorial Panel). J. B. Lippincott Company, Philadelphia, London, and Montreal. $3.50. xliii + 1159 pp. 1945.

The present edition of this comprehensive handbook follows the general plan of the earlier editions, although numerous alterations and additions have been incorporated to bring the work completely up to date. Both the theoretical and practical phases of nursing are covered by a wide variety of objective and essay type tests. For some of the objective type tests, line drawings have been used, the answers being given on the following page. New materials have been added to cover the recent advances in the knowledge of certain drugs and vitamins, and a table of common poisons and their antidotes has been provided.

Introductory chapters by Sister M. Berenice on hints to nurses preparing for State Boards, and by M. Cordelia Cowan on the purpose and value of State Board Exams, provide enlightening orientation for students preparing for their first experience with State Boards. The cover flaps carry useful lists of medical combining forms, and prefixes and suffixes relating to medical terminologies.

For nurses who are planning to take State Board

Examinations, or who are planning to return to the profession following a period of activity in some other field, the work will undoubtedly continue to be an extremely popular aid.

B. Aubrey Schneider

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American Medical Practice in the Perspectives of a Century. *Studies of the New York Academy of Medicine Committee on Medicine and the Changing Order.*

By Bernhard J. Stern. The Commonwealth Fund, New York. $1.50. xvi + 156 pp. 1945.

During the last hundred years American economy has changed from a rural and agricultural to an urban and industrial type. In medicine, scientific elements more and more replaced crude empiricism. Specialization became one of the basic characteristics of medicine; and doctors have tended increasingly to settle in urban areas, where hospital facilities, indispensable for this new type of medicine, are of easier access. Medicine has tremendously improved, but within the same period the cost of medical care, reflecting increased expenses for education and apparatus, has gone to unprecedented heights.

All of these changes and the new problems which they create for physician and patient are described in Stern's small book, which might be called a primer of medical economics. Stern's style is clear, his material well chosen. The New York Academy of Medicine is to be congratulated for sponsoring this book, the first of a series which, we hope, will live up to the expectations created by this first volume.

The strictly historical parts of the book are short but excellent. They represent a type of medical historiography of which we are in dire need, especially in the field of American medical history, where the "romantic" type, as Galdston calls it in his interesting preface, still prevails. It fills the medical historian with a certain melancholy when he has to state that so far we have been provided with good American medical history mainly by "laymen" (Stern, Deutsch, Shryock). It is to be hoped that these examples will eventually have a salutary influence on those medical men who make such laudable efforts to trace the history of their science and profession.

Erwin H. Ackerknecht

◆

Patients Have Families.

By Henry B. Richardson. The Commonwealth Fund, New York. $3.00. xx + 408 pp. 1945.

This exceedingly interesting book is devoted to an exposition of the abundant gaps in the understanding of individual patients brought about by inadequate appreciation of the fact that individual difficulties very often exist in a setting of family discord. The author has taken member by member, a few specific families who had visited at one time or another the out-patient departments of the New York Hospital, and out of these disjointed accounts of the separate members of each family, and by rather expert sleuthing on his own part and that of trained workers helping him, he has pieced together some very dramatic stories indeed. Not only this, but he has been able to penetrate behind the drama and to the motives at work, and so to help the individual patients to a relatively good adjustment, certainly to a better adjustment than ever would have been obtained by the piecemeal methods previously employed. The whole project, with the help of the Commonwealth Fund, was a joint effort with the Departments of Medicine and Psychiatry, the Macy Foundation, the Community Service Society, the Department of Public Health and Preventive Medicine, Cornell University Medical College, and the American Museum of Natural History,—the active work, I gather, having been performed by a small group of the Department of Medicine, Department of Psychiatry, and the Community Service Society. A great deal of work went into this project, and a kind of teamwork was fashioned that evidently grew in its effectiveness and understanding as the project went along. The method outlined in this book and exemplified in the records of the several families certainly presents an outstanding advance over the methods usually employed in our large hospitals, and a family clinic might very well be organized to take care of certain especially troublesome problems. Richardson, as an internist, has demonstrated a fine grasp of psychiatric principles of the more stable sort. One may suppose that he started with a considerable initial interest and developed his own insight as he went along. It is too bad that psychiatry and internal medicine have not more opportunity for just this sort of collaboration. It is an excellent book, to be read by every psychiatrist and internist.

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The Story of a Hospital: *The Neurological Institute of New York 1909–1938.*

By Charles A. Elsberg. Paul B. Hoeber, New York and London. $3.50. xii + 174 pp.; 25 plates. 1944.

This little book is a straightforward chronicle of the evolution of one of the pioneer institutions of medical specialization in this country. Dwelling more on administrative and personal than on medical data, it is rather a contribution to hospital history than to medical history. Giving the typical pattern of incessant change and heroic struggle against material difficulties, Elsberg's book will be a valuable source for those who study the history of the hospital in the U. S.

Ventures in Science of a Country Surgeon.

By Arthur E. Hertzler. Published by the author, Halstead, Kans. 304 pp. 1944.

A sort of autobiographical addendum by the author of *The Horse and Buggy Doctor*, this volume is built around his ventures in medical science, clinical and otherwise. The remarkable thing is that so busy and successful a practitioner should have been able to find so much time and energy for research and writing. His story is written in a breezy, entertaining, unliterary style. But the effort to maintain a continuous flow of wit and erudition frequently is so obvious that it is irksome. There is at least one glaring error of attribution—the repeated ascription to Kant of Descartes' famous "I think, therefore I am." Some of the author's pet aversions are the American Medical Association, social workers, socialized medicine, full-time workers in science and education, that part of the American population east of the Alleghanies, philosophy, and Chaucer. These sometimes are assaulted with more spleen than logic, but always in an entertaining manner.

◆

Introduction to Parasitology *With Special Reference to the Parasites of Man. Seventh Edition.*

By Asa C. Chandler. John Wiley and Sons, New York; Chapman and Hall, London. $5.00. x + 716 pp. 1944.

Without a doubt this is one of the most readable textbooks that is now available for an introductory course in parasitology. Chandler presents fundamental facts and principles of human parasitology in a clear, interesting manner, and has taken every opportunity to enliven the factual information with fascinating anecdotes and historical sidelights. Twenty-six years ago, when the author wrote the first edition, it was his wish to present the subject of parasitology in a manner to attract a wider group of readers than is usually attracted to the more conventional scientific textbook. It has been his belief that "scientific work flourishes best when intelligent public sentiment is behind it, and such sentiment is dependent upon capitalization of results already achieved, and a clear understanding of future goals." Although the present edition is a thoroughly scientific and scholarly treatise, it still retains the original freshness.

Usually, the subject of parasitology is restricted to the protozoa, helminths, and arthropods that cause or transmit disease. The author, however, has broadened the scope of his book to include the spirochetes, rickettsias, and filterable viruses. These have been included because they are frequently inadequately covered in bacteriology textbooks and are continually referred to in the discussion of arthropod vectors of disease.

The student is encouraged to consult the original literature by the author's practice of naming the investigators responsible for the more significant facts and opinions, and by the conveniently located complete references at the end of each chapter. The student's attention is also directed to lists of other books on parasitology, and to American and foreign journals that frequently publish articles on parasitology and related subjects. The author has the tendency to cite the more recent authority, if two investigators have demonstrated the same fact. For example, he refers to the work of Pipkins (1942) and not to that of Root (1921) in discussing the survival of *Endamoeba histolytica* within the house fly. When all of the authorities cannot be mentioned, it is, of course, debatable as to which should be excluded. Nevertheless, one must certainly commend the author for keeping up with the recent literature and for incorporating the significant findings in the present revision.

Laboratory techniques are not presented in great detail, so the book will not be found particularly suitable as a reference work for technicians. Nevertheless, all technicians concerned with parasitic diseases should certainly read the author's practical evaluations of diagnostic procedures and his emphatic plea for correct diagnoses. The following statement illustrates the author's stand on this matter, as well as his interesting style of writing: "As great danger lies in making a false positive diagnosis as a false negative one, for to inexperienced workers an ameba is an ameba, and often even epithelial cells and other objects are amebae. Many a patient, unfortunate enough to have an undiscriminating technician find an innocent *E. coli* or *Endolimax nana* in his stools, has had to submit to a course of treatment which was useless if not injurious to himself, and quite innocuous to the amebae. No doubt many patients with bacillary dysentery, having the numerous leucocytic cells diagnosed as amebae, have been sent to the grave or had their illness intensified by a toxic course of emetin which was entirely uncalled for."

The book is not as profusely illustrated as are some of the more recent textbooks on the same subject, but the three hundred odd figures that are presented have been well selected with but few exceptions, such as figure 52, on the life cycle of the malarial parasites, which pictures the sporozoites entering the red blood cells of man after inoculation by the mosquito. Although the author discusses the recent evidence against this direct penetration, his illustration is based upon the 1902 observations of Schaudinn that have never been confirmed.

Due to the clear presentation of facts about parasites and parasitic diseases, and above all, because of its ability to hold the interest of the reader, this edition should prove an excellent text for any course in parasitology where the subject is being presented to the student for the first time. It would seem to make little difference whether the course is being offered to undergraduate, graduate, medical, or veterinary students. Although the clinical symptoms of the various diseases are discussed, major emphasis is placed upon the biological aspects of parasitology. Regardless of the students' future application of parasitological knowledge, this biological foundation is essential for a clear understanding of the subject. More specialized information could be obtained by advanced courses and through the reading of the original literature.

M. M. BROOKE

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INFECTIOUS ANEMIAS DUE TO BARTONELLA AND RELATED RED CELL PARASITES. *Transactions of the American Philosophical Society, New Series, Volume XXXIII, Part III.*

By David Weinman. The American Philosophical Society, Philadelphia. $1.25 (paper). Pp. 243–350; 1 plate. 1944.

"One of the few exclusively American and exclusively tropical diseases, human bartonellosis has become an object of major concern in western South America. Causing at times alarming epidemics with high mortality, it is also established in widespread endemic centers. In such endemic foci it has an important effect on the health of the population, and from these centers the possibility of dissemination constitutes an everpresent hazard."

With the above statement, Weinman begins his discussion of the public health aspects of human bartonellosis, or Carrion's disease. Although today it is an acute problem only in certain areas of South America, it should not be considered as inherently restricted to its present geographical boundaries. The recent epidemic in Colombia, which was previously considered outside the endemic area, has demonstrated the ability of the disease to occur in or spread to other localities. This observation, coupled with increased air transportation and improved highway systems, should emphasize the future potentialities of the disease. The public health hazards of this disease make it imperative for the medical profession of the Western Hemisphere to become better informed regarding its clinical manifestations, transmission, and control.

During the thirty-five years since Barton first described the organism that is now known as *Bartonella bacilliformis*, an extensive literature has appeared on this and related organisms. In the present monograph, the author presents the first comprehensive summary of the existing information. The following are a few of the generally accepted facts regarding human bartonellosis. It exhibits two rather diverse clinical pictures: (1) Oroya fever, a severe, infectious febrile anemia, and (2) verruga peruana, a benign skin eruption. Both of these conditions are produced by the same etiological agent, which is now believed to belong to the bacteria rather than to the protozoa. Man and monkeys are the only vertebrate hosts known to be susceptible. Transmission is by means of *Phlebotomus* flies; contact and congenital transmission play a possible but minor role. There is no effective therapeutic agent available, and control is primarily concerned with anti-Phlebotomus methods.

Although it is valuable to have our present knowledge of the subject accurately summarized and evaluated, the most important contribution of this scholarly monograph is the attention that it attracts to the problems that remain to be solved. Why does Oroya fever develop in one person, verruga peruana in another, and no apparent symptoms in still others? The mechanism of the great blood loss is unexplained. Is it due to a toxin as yet not demonstrated? How frequently does the *Bartonella* entirely disappear from the infected individual and how often does it just pass into a latent state? Is the resistance to reinfection always dependent upon a latent infection or is there a marked degree of residual immunity after the sterilization of the parasite within the host? Then of course there is the critical need for a therapeutic agent that is capable of curing the disease and entirely ridding the body of the parasite. In addition, there are many unanswered questions concerning the insect vector and its host-parasite relationships. What is the localization of the *Bartonella* within the *Phlebotomus* fly? And is congenital transmission to its offspring possible? The ecological requirements of the vector are not fully understood. The lack of this knowledge retards the development of more efficient control methods. These are but a few of the problems that are raised by Weinman. Although they are discussed with regard to a specific organism, many of them are concerned with fundamental problems common to several parasitic diseases. There are enough urgent problems on bartonellosis to challenge the best efforts of clinicians, bacteriologists, pathologists, immunologists, entomologists, and sanitary engineers for many years to come.

In addition to the discussion of *Bartonella* and human bartonellosis, the author also surveys the present knowledge of two closely related groups of organisms, the Haemobartonellae and the Eperythrozoa. Weinman has personally contributed much to our understanding of these organisms and is particularly well qualified to discuss their significance. He was responsible for observing the essential difference between *Bartonella bacilliformis* and the Bartonella-like organisms of lower animals which led to the establishing of the genus *Haemobartonella.* Although these organisms are only known to infect lower animals, they have many properties in common with the human *Bartonella.* They are therefore invaluable as laboratory infections for control experiments. Several references are made to the *Grahamella* organisms, but a thorough review is not given. Inasmuch as they closely resemble the other organisms discussed, it would have been valuable if more information had been presented for the sake of comparison.

The monograph possesses an index, extensive bibliographies, and one plate. The plate pictures the morphology of *Bartonella bacilliformis*, *Haemobartonella microti*, and *Eperythrozoon coccoides*.

M. M. Brooke

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Microbes That Cripple.

By T. Arthur Turner, under the direction of Edward L. Compere. The National Society for Crippled Children, Inc., Elyria, Ohio. $2.50. xi + 241 pp. 1944.

Sufficiently accurate as to be authoritative, up-to-date and entertaining, but far from melodramatic, this book is of the sort seldom written and always needed. It presents problems factually in a straightforward manner. There is no eulogizing of the successes of medical science. There are chapters on the important crippling diseases or agents of diseases such as osteomyelitis, streptococci, tuberculosis, arthritis, virus infections, and syphilis. In each case the nature of the disease and its extent as a public health problem are considered, as well as something of its bacteriology, immunology, and epidemiology. There are also interesting and clear general discussions of infectious agents, of resistance to disease, and of recent advances in chemotherapy. The terrain, i.e., mainly the skeletal system, is described graphically. The concluding chapter on development of public health consciousness and modern services is excellent.

The book was apparently designed for persons concerned with rehabilitation work, teachers of crippled children, and others interested in problems of crippling diseases. However, it should be a valuable asset in the high school classroom, in elementary hygiene courses in college, and to all public health workers. It should be read by all intelligent people interested in community welfare.

It is easy to read. This slender volume is handsomely made; the type is large and clear and titles and subheadings are nicely set off. It is well written; rich, but not overly rich, in historical allusion; and at times it is humorous. Statistics are few and impressive. The numerous illustrations, some of which are in color, are particularly amusing and attractive and are mostly original drawings; they constitute a notable portion of the book. From the enormous amount of available material on the subjects considered, selection has been careful and well-balanced.

The index is adequate and the fairly extensive bibliography and fine 7-page glossary of terms should be helpful to the average reader.

Harriette Vera

Laboratory Manual for General Bacteriology.

By Department of Bacteriology and Immunology, University of Minnesota. W. B. Saunders Company, Philadelphia and London. $1.00 (paper). vi + 54 pp. 1945.

This manual was designed for use in an introductory course in general bacteriology. There are 29 exercises to be covered in 30 or 31 two-hour sessions of a quarter term or semester course. The scope is broad and includes exercises on such topics as soil and plant bacteriology, fungi, and water and milk analysis, as well as on pathogens and morphology. The selection of material for a first course in this field is always an extremely difficult matter, and teachers do disagree as to relative importance of subjects that could be included. There is a notable lack in this manual of any presentation of principles of disinfection and possibly there is undue emphasis on staining techniques and microscopy. A considerable number of exercises are devoted to pathogens, but there is none on anaerobic bacteria.

The directions seem to be clear, appropriate, and definite. There is a reasonable amount of explanatory material that should be of considerable help to the student new to the laboratory, and to the teacher as well.

Harriette Vera

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Travaux du Laboratoire de Microbiologie de la Faculté de Pharmacie de Nancy. *Fascicules XII (1939–1940–1941) and XIII (1942–1943–1944).*

Société d'Impressions Typographiques, Nancy. 112 pp. + 3 plates; 338 pp. + 10 plates. 1941; 1944.

Bulletin de l'Association des Diplômés de Microbiologie de la Faculté de Pharmacie de Nancy. *Numbers 24–25.*

Société d'Impressions Typographiques, Nancy. 76 pp. + 2 plates. 1942.

The two volumes of "Travaux" are reports of work carried on in France, during the war years, by Lasseur and his co-workers. The foreword of the earlier issue (XII) contains the statement that only part of the research accomplished is covered here. The destruction of cultures is mentioned in several places. The volume is, however, nicely printed on fine glazed paper. Most of the issue is taken up by a group of papers on agglutination and electric charge of dissociants of *Serratia*, *B. chlororaphis*, *B. lactis niger* and *B. mesentericus niger*. The second part, under the title of general microbiology, includes an article on the cultural characteristics of *B. mesentericus niger* and *B. lactis niger*, and two on conductibility of bacterial suspensions.

The later and larger volume, which is printed on very poor quality paper, states that the publication has been curtailed due to circumstances and that the work has been, for the most part, recorded without discussion or interpretation of results. Most of the number is devoted to the physiology of bacteria, to studies of chromogenesis in relation to the utilization of heavy metals and certain amino acids in culture media, or to illumination and irradiation of microorganisms. There are two articles on antigens and agglutination of *Chromobacterium chocolatum*.

The "Bulletin" contains rather brief scientific papers on serum coloration, by Roy and Boutaric; on microbial multiplication, by Regnier and Lory; and on a pneumatic micromanipulator and a study of *Leptospira* granules, by Bessemans, Wittebolle, and Baert. There are testimonials to Beijerinck, Ramon, Gorini and Weinberg, that to Weinberg being especially interesting because of his work on wound anaerobes during the first World War.

Harriette Vera

ANIMAL NUTRITION

The Avitaminoses. *The Chemical, Clinical and Pathological Aspects of the Vitamin Deficiency Diseases. Third Edition*
By Walter H. Eddy and Gilbert Dalldorf. The Williams & Wilkins Company, Baltimore. $4.50. xi + 438 pp.; 47 plates. 1944.

The new edition of this very excellent compilation has been "rearranged to sharpen the separation between the deficiency diseases and the chemical nature and functions of the vitamins," according to the authors in their preface. They have succeeded well in their task.

The book is divided into three main parts: Part I, The Vitamins; Part II, The Avitaminoses; Part III, Technical Methods of Vitamin Assay and Vitamin Values. The first part of the book includes an introductory chapter with an excellent table of "Postulated Vitamins," and another of "Some Vitamin Units and Reference Standards." This part then continues with a discussion of the chemical nature of the vitamins, their behavior and requirements. Then follow chapters on the nature and functions of the individual vitamins. Each of these chapters contains a brief historical introduction to the discovery of the vitamin, and then discusses its nature and its function.

Part II contains chapters discussing in detail each of the vitamin deficiencies, again including historical information. In these chapters a clear differentiation is made between the symptoms produced in experimental animals and those exhibited by humans. Excellent pictures illustrating deficiency symptoms are included in the book, as well as histological sections. The chapters have subdivisions which are valuable in organizing the information.

Part III has to do with vitamin assay methods. These chapters are brief and merely discuss the type of test used, with references to the original literature.

At the end of the book, there is a complete bibliography arranged according to chapters. Following the bibliography, there are tables showing the vitamin values of many of the common foods. A subject index follows this. The book is well written and contains a wealth of information, well organized and accurate. Much new data has been included. It will be an invaluable volume for nutritionists.

Marguerite M. Schmidt

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Honey and Your Health. *A Nutrimental, Medicinal and Historical Commentary. New and Revised Edition.*
By Bodog F. Beck and Doree Smedley. Robert M. McBride and Company, New York. $3.00. 246 pp. 1944.

Few in this era of cane sugar realize what an important article in the diet honey was, up until modern times. Sacred for its nutritive and medicinal properties, the source of exuberance in the form of mead, honey was of paramount importance to the ancients. The authors of this book have collected an immense amount of entertaining lore about honey, and this forms the most valuable portion of *Honey and Your Health*. As to the relation of honey to health in modern times, they have not succeeded so well, largely because of the exuberant enthusiasm for their subject, perhaps inspired by one or another of the numerous ways of eating and drinking it for which they give recipes. The fact is that they are uncritical about the claims they make of its virtues. There is no doubt whatever that Americans (at least prior to the present sugar shortage) eat altogether too much cane-sugar for their welfare; nor is it disputable that honey (largely levulose and dextrose) is more rapidly assimilated. It is probably also valid to reason that honey is less likely to be injurious than sucrose because there is less temptation to over-indulge in it—satiation comes sooner. But it is surely going altogether too far to say that cane sugar is a drug and not a food, that it has calorie content that will provide heat and energy but that it does not provide nourishment; that "artificial [sic] sugars. . .oxidize violently in the human stomach. . .with an explosive effect that obliges the vital organs suddenly to work harder and faster"; that these artificial sugars and starch produce poisons and cause chronic fatigue, kidney and circulatory disorders, etc., while honey is not oxidized by the digestive tract and is nutritious, being converted to essential glycogen. This is twisting things with a vengeance. The authors would have made out a much stronger case had they been more moderate in their claims.

A matter for surprise is the complete omission of any real account of the life of the honeybee or of its honey-making. To sum up, this book is an interesting and useful compilation of lore about honey, but biologically it is uncritical, not to say unsound, and omits the central biological story of honey almost entirely.

Bentley Glass

BIOCHEMISTRY

Physical Chemistry for Students of Biology and Medicine. *Third Edition, Second Printing.*

By David Ingersoll Hitchcock. Charles C. Thomas, Springfield and Baltimore. $3.50. xiii + 264 pp. 1940; 1944.

Clear in its treatment of topics selected for their applicability to biological problems, this text is outstanding in its field. The scope of the book is purposely limited largely to a consideration of the physical chemistry of dilute aqueous solutions, since, as most will agree, an understanding of the laws of dilute solutions is fundamental to that of newer developments. One touchstone of the excellence of such books as this is their treatment of osmosis. In the present case this leaves little to be desired, as it is clear, concise, and accurate. The treatment of electrochemistry has been expanded and rewritten, and now forms a sequence of six chapters. These are followed by chapters on colloid chemistry, membrane equilibrium and potentials, equilibria in blood, reaction velocity and enzyme action, and transformations of energy. These topics are all discussed in merely introductory fashion. The use of mathematics is held to a minimum throughout. At the end of the book is a series of 20 laboratory experiments, eight of these being newly added exercises in electrochemistry.

Many of the fields of newer importance to biology are not included. There is, for example, no discussion of the nature of the chemical bond in the light of recent theory, of rheological phenomena, of x-ray diffraction analysis and the structure of proteins, of absorption spectra, of tactoids, etc. The entire field of the effects of radiation upon chemical structure, so important in modern biology, is ignored. These remarks are not intended as criticism of a most valuable introductory text. It is, however, worth pointing out that the original selection from the vast field of physical chemistry of those topics most important to biologists must be subject to change as the trends of modern biology themselves alter.

Bentley Glass

Untersuchungen über Aminosäuren, Polypeptide und Proteine. *Volume 1, 1899–1906. Volume 2, 1907–1919.*

By Emil Fischer. Volume 2 edited by M. Bergmann. (Julius Springer, Berlin); J. W. Edwards, Ann Arbor, Michigan. $38.00. x + 770 pp. (vol. 1); ix + 922 pp. (vol. 2). (1906; 1923); 1944.

In these two volumes are collected the 160 publications of Emil Fischer and his students on the chemistry of proteins and products derived from them. The experimental work that is recorded here forms the foundation for most of our knowledge of the organic chemistry of protein molecules.

Fischer's teacher, Von Baeyer, was engrossed in studying the structure and syntheses of dyes; but Fischer's interest turned to those organic compounds which constitute living matter, and he devoted his life to the study of sugars, proteins, purines, and the steric arrangements of these molecules. The scope and importance of his contributions in these fields are unique in the history of chemistry. The reports of his research on sugars fill two additional volumes—and this work is fully as important and perhaps better known than his contributions on proteins. Another volume is required to collect the results of his studies on purines.

Individual articles from the collected protein papers are not in themselves impressive. Each one deals concisely with some specific preparation—the digestion of an albumen; the isolation of an amino acid from such a digest; a chemical synthesis of an amino acid; the resolution of this amino acid into its optically active forms; the combination of two or more amino acids into polypeptides; etc. Consequently in going through the titles and even in reading the articles, one is hardly aware that here proline and hydroxyproline are being isolated for the first time, that the first chemical synthesis of serine is being reported, that racemic mixtures of amino acids are being resolved for the first time into their active antipodes, or that a polypeptide of 18 amino acid units (the most successful attempt at *in vitro* protein synthesis yet achieved) has been accomplished.

In all this work there is nothing really revolutionary, nor any dramatic discovery. Yet, when the individual contributions are reviewed as a whole, the epic nature of the work stands out, and one can see the aggressive and logical attack that Fischer made on the problem with all the organic and biological techniques inherited from the previous generation of famous German chemists.

There is included, with these experimental publications, the manuscript of an address on protein chemistry given in 1906 before the Deutschen Chemischen Gesellschaft, which is of interest because it so clearly outlines the exact status of the progress that had been made up to that time.

In his writings, Fischer used a style which is more modest, direct, and concise than is often found in German scientific literature. For this reason the articles are easy to read or translate, as is evidenced by their popularity with graduate students taking language examinations.

ROBERT E. EAKIN

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A LABORATORY MANUAL OF PHYSIOLOGICAL CHEMISTRY. *Fifth Edition.*

By D. Wright Wilson. The Williams & Wilkins Company, Baltimore. $2.50. 269 pp. 1944.

This teaching manual contains many fine laboratory experiments in physiological chemistry. Part I of the manual is considered "Introduction." It contains procedures for the determination of inorganic constituents, for the preparation of standard acids and alkalis, for the determination of electrolytic dissociation, and for the study of colloids, alcohols, aldehydes and esters, carbohydrates, proteins, and fats. The directions for these are clearly written, and some include a brief discussion of the theory of the procedure. The tests which have been selected are a review of procedures in other courses, but with particular emphasis on those associated with biological material.

Part II of the manual contains procedures on body tissues and fluids. Here we find a study of saliva, gastric and pancreatic juice, milk, blood—general and qualitative, bone, muscle, the cell nucleus, bile, urine—qualitative, normal and pathological, and quantitative. There are also included diets for the study of dietary deficiencies, a table of logarithms, and an abridged table of atomic weights. As in part I, the experiments are well chosen, directions are clearly written, and there is some discussion of theory. References to the original literature are also included. Directions for making various solutions are included in footnotes.

The printed matter is all on the left hand pages, the right hand pages being left blank for recording the results. The manual is one which could be adapted for use in any course of biochemistry. It has many experiments, use of which can be limited as the needs of the students demand.

MARGUERITE M. SCHMIDT

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FUNDAMENTALS OF INORGANIC, ORGANIC AND BIOLOGICAL CHEMISTRY, *with pamphlet, An Outline for Teachers.*

By Joseph I. Routh. W. B. Saunders Company, Philadelphia and London. $2.25. vii + 274 pp. 1945.

This text has been written primarily for use in teaching chemistry to nurses. As the title implies, it includes the fundamentals of inorganic, organic, and biological chemistry. In itself, the text is clearly written and well expressed. However, in his effort to include only the absolute essentials in inorganic and organic chemistry for an understanding of biological chemistry, the author has omitted some of the essentials necessary for accurate information, particularly in inorganic material. The discussion of valence and oxidation-reduction is not well done. The chapters on biological chemistry are full, containing much information—more than is necessary for a nursing course. While one may agree with the author, in his preface, that students respond better to biological chemistry, and that such information is more necessary for nurses, yet for an adequate understanding a more thorough background than Routh gives is necessary. The book might be a satisfactory text for a group who have had a year of thoroughly taught inorganic chemistry. The teacher's outline is adequate for a novice, and will aid in outlining the work for her.

MARGUERITE M. SCHMIDT

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OUTLINE OF THE AMINO ACIDS AND PROTEINS.

Edited by Melville Sahyun. Reinhold Publishing Corporation, New York. $4.00. 251 pp. 1944.

At the present time there is great interest in proteins and amino acids. This book is a concise, readable outline of this field, now finding application in practically all branches of biology. Clarity and simplicity have been achieved by touching lightly on the complicated theoretical and argumentative aspects of the subject. These have been covered by the larger treatises mentioned in the adequate bibliographies at the end of each chapter.

The twelve chapters cover the whole field of protein chemistry, from the account of the discovery of the amino acids to the metabolic and nutritious aspects of amino acids and proteins. It contains chapters on the structure and hydrolysis of proteins as well as on their synthesis and methods of analysis. For biologists who are not specializing in this field, the book represents the most efficient means of bringing their knowledge up to date. It will also be of value, however, to those who wish to obtain the necessary background for intensive study. It is a simple, readable presentation of the essential and fundamental aspects of the subject.

FRANK H. J. FIGGE

◆

ENERGY RELATIONSHIPS IN ENZYME REACTIONS. *Annals of the New York Academy of Sciences Volume XLV, Art. 9.*

By Joseph S. Fruton, Eric G. Ball, Max Bergmann, Herman M. Kalckar, Otto Meyerhof, and Carl V. Smythe. New York Academy of Sciences, New York. $1.00 (paper). Pp. 357–436. 1944.

This is a series of papers which resulted from a conference on energy relationships in enzyme reactions held by the section in physics and chemistry of the New York Academy of Sciences in February, 1944. At first sight, the title of this symposium would make it appear that this was a premature discussion of a subject about which little is known. The papers show, however, that some advancement has been made, "so that probing fingers are already beginning to search for the mechanism whereby this energy release is geared to perform the functions essential to life."

The introduction is a concise summary of our present knowledge of enzymes. The most provocative and at the same time most informative paper in the series is that by Ball, on the energy relationships of the oxidative enzymes. The discussion of energy relationships in glycolysis and phosphorylation is concerned chiefly with the complicated subject of muscle metabolism and is marred by the author's egotism. The significance of coupled reactions for the enzymatic hydrolysis and synthesis of proteins, discussed by Bergmann and Fruton, is both timely and excellent. "From the experimental results and the speculative considerations which have been presented in this paper, it follows that future progress on the problem of the biosynthesis of proteins and peptides depends on a more intensive investigation of coupled reactions with well-defined enzyme systems and with substrates of known structure." The final paper, on some enzyme reactions of sulfur compounds, is a speculative account of the metabolism of methionine, cysteine, glutathione, and other sulfur compounds.

Frank H. J. Figge

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The Chemistry and Technology of Food and Food Products. *Volume II.*

Edited by Morris B. Jacobs. Interscience Publishers, New York. $10.50 (both volumes—$19.00). xx + 890 pp. 1944.

This is the second volume containing the concluding sections of an exhaustive treatment of the chemistry and technology of food and food products. The first volume was reviewed in the March, 1945, number of this journal (20: 101).

Part III is a general discussion of large scale unit operations and processes. The general facts relating to sanitation and quality control of food are adequately covered in six chapters in Part IV. This includes a consideration of Governmental agencies and regulations, food grading and food machines, detergents and sanitation, the control of insects, molds, and rodents. Part V is a comprehensive survey of the general and specific methods of preserving and packaging food. The final section deals with the production of cereal grain products, sugar, confectionery, jams, and jellies, milk and milk products, meat, and alcoholic and nonalcoholic beverages. The methods used to treat water which is to be used for drinking and manufacturing purposes are also described in detail.

In general this will be a useful reference book for food technologists of all classes. Specialists in this field may occasionally have to consult the references cited for specific details. The value of such a reference work depends on how carefully and thoroughly the subject index has been prepared. Extensive use of the index, which covers 55 pages of fine print, has convinced the reviewer that this is one of the best features of the book.

Frank H. J. Figge

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PSYCHOLOGY AND ANIMAL BEHAVIOR

History of Psychology *From the Standpoint of a Thomist.*

By Robert Edward Brennan. The Macmillan Company, New York. $3.00. xvi + 277 pp. 1945.

The author has stated what may be called a four-fold purpose for his book in his Prologue: first, to correct false notions of what psychology is by showing that its real business is "the study of human nature" rather than either mind reading or psychoanalyzing; second, "to relate the tale of psychology in a strictly traditional manner"—which no other book, to his knowledge, has attempted to do—"...an interpretation or a point of view that Aristotle or Thomas Aquinas might have given us, were they able to look back like ourselves, over the perspective of nearly three thousand years' development"; third, to show that the "story of psychology has a philosophic as well as a scientific background—far more of a philosophic one," which most chronicles of today hardly show "due to a positivistic prejudice," that is, "to a conscious or unconscious attitude, on the part of certain scientists, which presumes that philosophy has nothing to contribute to the field of psychology"; and fourth, to declare his dissatisfaction with the way in which the story of psychology has been told heretofore, and to point out the possibility of a new way of approaching its contents, although recognizing the inadequacy unavoidable in so short a space. He claims "that all the factual data that have accumulated in the laboratories and clinical chambers over the past half century, can be placed only in one tradition, so far as their philosophic significance is concerned, the tradition of Aristotle and Thomas Aquinas." This he attempts to prove. He admits that in the effort to be brief he may have fallen into the vice of obscurity.

From the two ways of approaching the study of man, the scientific and the philosophic, he arrives at a definition of psychology which embodies the two, as "the study of acts, powers, habits, and nature of man" from the phenomenal, or "empiriological," and the noumenal, or "ontological," standpoints.

In his chapter on "The Thomistic Synthesis" we have what, judging from the subtitle of the book, the author regards as its heart. The synthesis of Aquinas he considers remarkable on two scores: first, he "linked together all the scattered and often fragmentary insights into reality" of the preceding thinkers into an organic whole; and, secondly, he was able to add to the actual content of philosophic knowledge by his own profound analyses." Moreover, Aquinas "was able to perfect the method of the schools, by consecrating to the service of truth the dialectical skill which the rationalists so highly praised and which the mystics so roundly condemned." In a way analogous to that of Aristotle mentioned above, "Aquinas distinguished human from divine wisdom at the same time that he showed the basic continuity of philosophic and theological experience in the total content of man's knowledge."

In his presentation of "The Core of the Thomistic Psychology," the author should be quoted, perhaps, rather than paraphrased· "What Aquinas did for philosophy in general he did for psychology in particular. Here the thing that characterizes his work is the new spirit with which he addressed himself to the task of analyzing the nature of man in the light of Aristotle's hylomorphic doctrine. In his psychology we can discover Platonic elements as well as the substantial features that were Aristotelian. With a like sense of impartiality, he sought to discover the possible uses of the Augustinian doctrines that were common in his day. Nor did he disdain to consult the Jewish and Arabian commentators for the solution of his problems. He worked on the principle that all knowledge and all truth, whatever its source, is capable of harmonious adjustment." "The solution of the major issues of psychology in Aquinas's day demanded that the body-soul problem be given first place. Aristotle had merely declared that the true solution was so obvious as to make clarification superfluous, beyond a mere statement of the fact of the substantial union of these two basic principles of human nature. Not so Aquinas! He insists on a demonstration; and his emphasis on the necessity of proving this central assumption in the Aristotelian psychology, shows, I should say, that he was much closer to the temper of modern psychology and more appreciative of its needs than was Aristotle himself. The question here, to be sure, is merely one of focus" (pp. 62–63).

There are three great trends of thought that have dominated the historical development of psychology from the days of the Greeks: the tradition of Democritus, which is the spirit of materialism—holding that only matter is a valid object of study; the idealistic one of Plato—that only mind is a valid object of knowledge, because only mind is real; and the Aristotelian, in which both mind and matter are knowable, because both are real, and man is knowable because he is a form immersed in matter, a form "in which both body and soul are joined as essential elements."

It is Aristotle's tradition "which is emerging today with new depth and vigor when confronted with the impartial evidence of the investigators. More than ever before, we realize now that the observed facts of consciousness must be correlated with the physiology of human life if they are to be correctly understood." Furthermore, "that the mechanistic concept of the soul as a property of cortical substances or the Cartesian notion of it as an immaterial entity whose whole nature is to think, must be ruled out." Such ideas "do not fit the evidence." If any solid advance is to be made in the field of psychophysical analysis, it must be on the principle that "the soul of man, like the first actuality of all other cosmic creatures, is a form united substantially with matter." "This being the case, psychology cannot limit itself to the phenomena of consciousness, but must extend its technical observation to the *whole man*" (pp. 252–3).

The author's treatment of the numerous "traditions" and schools, from the days of Aquinas down to the present, is necessarily brief and concise. He tries to evaluate them in a fair-minded manner, although, of course, we should hardly expect the followers of any one school to be wholly satisfied with the fulness of treatment, even if they feel that the evaluation is fair.

The book, though short, clearly and interestingly written, and one which fills a special need in the field of psychology, requires of the reader a good background in philosophy and psychology for an adequate appreciation of the full story of psychlogy which it presents. It should serve well for both a pre-view and a review for those with the foundations; but it could hardly be considered as a primer. Supplemented with selected readings from the many sources drawn upon by the author and listed in the Bibliographical Index and the Bibliography, it might well be used as a textbook in undergraduate classes. For this purpose, however, a bibliography of detailed selections from the sources might well be provided for each chapter, together with a list of questions to guide the student in his readings.

C. Hart Westbrook

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PSYCHOLOGY.

By Floyd C. Dockeray. Prentice-Hall, Inc., New York. $3.00. xiv + 504 pp. 1944.

This is the fifth printing of the popular textbook first printed in April, 1942. The author's purpose for this text has been "to help the student to understand human behavior, and, second, to encourage him to practice those principles which apply to his own case." Recently authors have had to meet this problem, as psychology has grown more popular and teachers have tried to make it more interesting to pupils by the use of applications to their everyday life, while at the same time acquainting them with the known facts of psychological research and investigation, the methods used, and the "development of generalizations or principles." How can one present the subject as a scientific discipline yet make it "interesting," show its practical applications, and, perhaps, give students an opportunity to study themselves in an elementary way and understand the meaning and the significance of the terms, symptoms, and disorders found in abnormal psychology, and so widely bandied about in the press and popular magazines? It seems that the author has stood by his chief aim of presenting psychology as a scientific subject very well, and has given adequate attention to the other demands without going too far towards over-popularization. His text has already been widely used and highly spoken of.

C. HART WESTBROOK

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THE BASIC TEACHINGS OF THE GREAT PSYCHOLOGISTS.
By S. Stansfeld Sargent. The New Home Library, New York. 69 cents. xiv + 346 pp. 1944.

This book surveys the entire field of psychology aspect by aspect, from a historical point of view. It is a sound and useful reference or introduction, although too condensed to permit real insight into any one phase. For example, Freudianism . gets approximately six pages, along with some scattered references, and the work of G. Stanley Hall and J. B. Watson two or three pages between them. In the generally good chapter on the effect of heredity and environment, there are a number of erroneous or questionable statements. such as the one that "only two mental abnormalities definitely are inherited—feeblemindedness and Huntington's chorea." For a bird's eye view of historical psychology, the book will prove useful for students and laymen. Its exposition is clear and simple, although its style is rather undistinguished. Its organization is logical and effective.

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DVORINE COLOR PERCEPTION TESTING CHARTS. *Volume 1.*
DVORINE COLOR PERCEPTION TRAINING CHARTS. *Volume 2.*
By Israel Dvorine. Published by the Author, Baltimore (2328 Eutaw Place). $25.00. Volume 1, 1 rotating disk and 60 color charts; Volume 2, 4 color plates and 70 color charts; instruction manual (paper), 24 pp. 1944.

The charts included in these two volumes follow the conventional plan which was introduced by Stilling, adopted by Ishihara, and extended in the Test published by the American Optical Company. Since the reading of numbers or letters on charts of the Stilling type is dependent on a differential in brightness between the colors on a chart and not on a differential in hue, such chart-tests cannot be considered reliable. It is true that a change in brightness differentials in the vision of a "color-blind" person is often associated with a change in hue-differential; but some persons who fail the chart-tests have no difficulty in distinguishing hues, even the hues of the numbers they cannot read; while some who can read the numbers on the charts are seriously "color-blind."

It has often been pointed out that the inclusion in the sets of charts which the "color-blind" person can read, but which persons with "normal" color vision cannot read, indicates clearly that the reading is not based on differences in hues, but is based on differences in brightness. Some "color-blind" individuals can read the charts which "normals" are supposed to read, because the luminosity-thresholds of the critical hues have altered so much that the numbers, which for the "normals" are brighter than the surrounding spots (constituting the background), are for them darker than the background; and vice versa, for other charts.

Two features of Dvorine's volumes merit attention. The first feature is inclusion of materials for testing the accuracy of naming of colors; and color naming is undoubtedly important. In highway traffic, for example, the light which is seen by drivers with "normal" color-vision as green, may be seen by a color-blind driver as a slightly greenish blue; if the driver, however, has learned to call the color "green" he knows that it means "go." Similarly, if the light which "normals" see as red is called "red" by the "color-blind" driver, although he may see it actually as orange, he knows the light means "stop," and is no danger. A color-blind driver who names the lights as do persons of "normal" color-vision may even be a safer driver than are many "normals."

There are two difficulties involved in Dvorine's charts for training color perception. One is the omission of the names by which the colors should be called. It is well known that persons of "normal" color-vision differ from one another in the names they apply to colors, especially to colors of low saturation. Hence the validity of the training depends upon the names applied by the particular trainer. The second difficulty is that a really color-blind person would be trained to call the colors by names of colors he does not actually see; this would confuse him and cause him trouble in traffic.

The second important feature of Dvorine's presentation is the assumption that color-vision can be improved by training. We admit that color-naming can be improved by training; but that the fundamental features of so-called "color-blindness" can be modified by training is merely an hypothesis. We know that a "color-blind" person can learn all the charts in a set; calling off the numbers correctly, although remaining unable actually to see the numbers on many of the charts. One young man memorized all the charts in the A. O. C. set, and then admitted that there were many numbers which he could not see. After a course of treatment with Vitamin-A and cobra venom, his color perception improved greatly.

That training may produce a slight improvement initially, due to adjustment to the test situation, assisted by better attention, is true; but beyond that point the usefulness of training in color perception is conjectural. However, Dvorine is to be commended for publishing the first set of charts by the use of which his theory can be experimentally tested.

KNIGHT DUNLAP

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THE PSYCHOLOGY OF DIET AND NUTRITION.

By Lowell S. Selling and Mary Anna S. Ferraro. W. W. Norton and Company, Inc., New York. $2.75. 192 pp. 1945.

It is somewhat surprising that a scientific psychology has not grown up about the problems of food and eating. The psychology of sex is a highly developed field, yet food and the need for eating, along with hunger and appetite, are more omnipresent than sexual motivation. Why people form improper eating habits and why they do not eat suitable diets when these are available are questions that have assumed double importance in wartime. The nutritionist can prescribe an adequate or an optimum diet, but to make people follow it is a psychological problem of no mean order. *The Psychology of Diet and Nutrition,* written jointly by a psychiatrist and a dietitian, is an excellent preliminary approach to the study of these difficulties. The topics considered are: The Basic Psychology of Nutrition; Food Habits, Fads, Customs, and Aversions; Children's Feeding Problems; Feeding Problems Due to Psychological Maladjustments; The Dietary Significance of Mental Disorders; Food and Nutrition as They Affect the Home; Mental-Hygiene Technique Applied to the Feeding of Large Groups; The Special Psychology of the Patient on a Diet; The Effect of Improper Diet on Behavior and Personality; and Educating the Consumer.

These chapters are excellent, singly or as a whole. They are logically organized and clearly discussed, full of interest and helpful suggestion. There is an index. The volume will be of primary interest to nutritionists, doctors, psychiatrists, and psychologists, but it may also be recommended without reserve to the layman, the mother, indeed to all those concerned with provisioning or the preparation of food.

BENTLEY GLASS

HANDBOOK OF INDUSTRIAL PSYCHOLOGY.

By May Smith. Philosophical Library, New York. $5.00. 304 pp. 1944.

This book should appeal to persons in any walk of life who have contacts with those who live and work in industry. And now that industrial reconversion is upon us as well as the vocational guidance and rehabilitation of our returning service men and women, persons who are in applied psychology and those preparing to enter upon it, social workers, school psychologists, and medical practitioners, particularly, will find it useful. Those in industrial medicine, will find this an informing, stimulating, and interesting book.

The chapters deal with: Pioneer Work; Fatigue in Industry; The Environment (General and Material—Light, Temperature, Noise, Hours; Psychological—The Group, Mental Atmosphere, People in Authority); Finding the Job for the Person and the Person for the Job; Time and Motion Study; Temperaments, particularly the Nervous—Must the Nervous Person Break Down?; Why We Work—Some Symptoms of Something Wrong—Are Accidents Accidental?—Breakages—Grievances—Misfits—Sickness; Measures of Human Well-being (Absence through Sickness—Labor Wastages); General Hints in Methods of Investigating; Conclusion.

The interplay of the workers' psychological factors with the physical and environmental factors is especially well presented in the chapters entitled "Temperaments, Particularly the Nervous" and "Why We Work," on the basis of actual and recent industrial studies. Physicians, as well as foremen, managers, and industrialists will find these facts and principles and motivations to work significant. The author herself conducted the investigations of the nervous temperament and its influence upon efficiency and sickness.

The data used and interpreted are drawn mainly from the researches and investigations begun by the British Health of Munitions Workers' Committee and its successor, in 1919, the Industrial Fatigue (later, Health) Research Board, in connection with World War I's problems, and continued in many industries through the years of peace down into those of World War II. The Medical Research Council's Special Reports, the Journal of the National Institute of Industrial Psychology, and other journals have supplemented the earlier reports. And for these reasons the data are especially valuable and suggestive. Comparatively few tables are used, and they are short. Such data as are given are interpreted for the reader in the text itself in terms of percentages and hence are quickly and easily grasped. The book is a scientific production presenting scientifically planned and conducted studies, but is not technically dry.

The individual in his group, and at his job, is investigated or experimented with in such a way as to enable doctors, industrial managers, or others, to study him as a whole human being in his social and his objective or work environment. And since certain of the mechanical factors can be regulated and studied very objectively and accurately, the part which these play in the psychosomatic situation can be more readily determined. This phase of applied psychology is rapidly growing in its exactness and value, and laymen, including the industrial and office workers themselves, should become familiar with the findings and their practical help.

C. Hart Westbrook

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PRINCIPLES AND PRACTICE OF REHABILITATION.

By John Eisele Davis. A. S. Barnes and Company, New York. $3.00. xxi + 211 pp. 1943.

This is a presentation in a rather didactic, pedantic way of the general topic of rehabilitation as applied particularly to psychoses and psychoneuroses. There are fairly adequate chapters on diagnostic criteria, psychological approach to the problem, interest and effort theories, modern methods, therapeutic objectives, handicraft, education and art, and there is a great deal of common sense observation and deduction exhibited in these chapters. Nevertheless, the book is hard to read. The actual literary style is exceedingly difficult, at times so much so that the meaning is quite unclear. Furthermore, it is laden down with references in the text itself to what various physicians of considerable standing have thought about all kinds of problems having any bearing at all on the final problem of rehabilitation, so that one is lost in the details of accessory material. It seems that the principles and practice of rehabilitation ought to be reducible to a much clearer and much simpler statement. Nevertheless, practitioners of rehabilitation may gain some help from the book.

Wendell Muncie

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SOLDIER TO CIVILIAN. *Problems of Readjustment.*

By George K. Pratt. Foreword by George S. Stevenson. Whittlesey House, McGraw-Hill Book Company, New York and London. $2.50. xii + 233 pp. 1944.

This is a very sensible account of the problems confronting the soldier who returns to civilian life, and conversely of those civilians who have a soldier returning to them, in the home, in industry, and in society generally. The problem of adjustment to the Army and the reverse problem are both very well presented, in terms which anybody can understand, and devoid of that sloppy sentimentality and scarehead stuff which has characterized a great deal of writing on the subject in recent months. The author has had extensive experience, both as an officer in World War I and in veterans' work and general mental hygiene activity, is thoroughly qualified to present the subject, and has done an excellent job.

Wendell Muncie

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PERSONAL MENTAL HYGIENE.

By Dom Thomas Verner Moore. Grune and Stratton, New York. $4.00. vii + 331 pp. 1944.

A proper addition to the title of this book would be "for Catholics," since the author is a well known priest as well as psychologist and psychiatrist. The book has been passed through official Catholic censorship and contains statements and attitudes which would find general approval only in a Catholic society. This attitude is evident throughout in the appeal to a type of self-discipline to overcome various emotional difficulties, depression, anxiety, scrupulosity, etc. It reaches rather absurd proportions when the author takes Oliver Goldsmith to task, pointing out that poor Oliver might have led a happier life if he had only been less impulsive and had kept himself under better control in several ways. What the likely effect of this would have been on Oliver's poetry isn't noted. One may suppose also that Father Moore would find the same fault with Mozart. Why couldn't Mozart be satisfied in the services of the Archbishop of Salzburg, as his father so often implored him to be? In the light of history it appears completely unimportant that Goldsmith and Mozart were personally unhappy. Much more important is the likely fact that out of their unhappiness there developed a creative urge which has rarely been equalled.

Such attitudes noted above reach their apotheosis, however, in the chapter on "The Mental Hygiene of the Home." It takes a very special kind of bias to make such statements as the following: "Morality needs no customs for the source of its principles. Were all history destroyed, the fundamental relations of man to man in the existing social order would supply the material from which reason sitting in judgment on conduct would derive the necessary natural principles of the moral order. And action in accordance with these principles would constitute the essence of sound mental hygiene." Also, "To plan a marriage without children is in itself a crime. It is true that marriage is essentially a pact of perfect friendship, and because of this fact circumstances may arise that would justify a marriage when children would not be possible. But speaking of ordinary conditions a marriage without children is not to be contemplated. Mechanical methods of contraception are inherently wrong, and one is not allowed to practice the biological method of rhythm merely to avoid the burden of children." Also, "Divorce is always a tragedy," and concerning the "disintegration of family life," the following: "The stability of the family in the Middle Ages rested to a large extent (1) on the law of charity governing the relations between parents and children, (2) on the Catholic doctrine of the indissolubility of the marriage tie, and (3) on the general concepts of duties and obligations existing between all members of the social order. With the advent of the Reformation, there extended into all spheres of life a tendency to deny the existence of authority and throw aside the ancient regard for all obligations and so exert the supremacy of the individual and his right to satisfy his personal desires. After ecclesiastical authority had been called in question, it was only natural that the existence of civil authority should be denied. And if there is no such thing as church or state authority, parental authority is easily disregarded." It need only be stated that these concepts will find general acceptance only in a Catholic society.

The most disturbing part of the book, however, is the revelation of the author's attitude toward his own profession, psychology. "We are confronted with the hopelessness of psychology. Religion alone can here open the way to sublimation that will transcend all the difficulties of life and the final failure of death. If mankind is to establish in society a stable mental peace it must come about by the realization that all nations and peoples constitute one single social order, that in this social order God is the infinite intelligence in a universe of intelligent beings. . .that every human being has a work to do in the world and when it is done he will attain to the knowledge of truth. . . ." One may wonder why such an intelligent attitude toward a world order and world peace has to be labelled as a religious concept. Father Moore apparently operates in a field of psychology which he conceives as a small area operating under a superstate of religion. It is not likely that this view will receive general approval from professional psychologists.

Actually, there is in this book a great deal of common sense advice that is of practical value. The appeal to the exercise of personal discipline is valuable, but would be much more valuable still if the author could have avoided the mistake of assuming that the understanding of the emotional life as practised in the best psychiatric circles is the equivalent of a ticket of admission to unlicensed emotional expression. Most of us feel that discipline and control are best established only in a setting of understanding.

WENDELL MUNCIE

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MENTAL ABNORMALITY AND CRIME. *Introductory Essays. English Studies in Criminal Science, Volume II.*
Edited by L. Radzinowicz and J. W. C. Turner. Prefaced by P. H. Winfield. Macmillan and Company, London. $3.75. xxiv + 316 pp. 1944.

This is a compendium written, at the suggestion of members of the Law School of Cambridge University, by outstanding specialists in psychiatry and criminology in Great Britain. There are thirteen chapters with almost as many authors, each contributing a little monograph in itself. The titles of the chapters indicate the scope of the work—mental variations and criminal behavior, psychoses and criminal responsibility, psychoneurosis and criminal behavior, mental deficiency, psychopathic constitution, functional nervous disorders after injury, physical factors, alcoholism, sexual offenders, juvenile delinquency, reaction to military life and criminal behavior, the diagnosis and treatment of delinquency, and finally a report on the work of the Exeter Child Guidance Clinic. This is an excellent statement of a conservative sort concerning the various aspects of the problems of criminal behavior, if rather short on the treatment aspects.

WENDELL MUNCIE

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BRAINSTORM.
By Carlton Brown. Farrar and Rinehart, New York and Toronto. $2.75. 302 pp. 1944.

This is an autobiography—the story of a psychosis and efforts at treatment and recovery. From the scientific standpoint it would seem that the diagnosis of dementia praecox, made at the first psychiatric hospital, was quite wrong. The account appears full of affective elements of elation, and the manner of recovery would point to the same diagnosis. What good this kind of a book does is hard to see. It is hard to see also where the author's enthusiasm for psychoanalysis comes from, because it appears not to have been used in his case at all. Maybe that is why he is enthusiastic about it, as the methods that were used seem to have contributed so little to his recovery.

WENDELL MUNCIE

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FREUD: *Master and Friend.*
By Hanns Sachs. Harvard University Press, Cambridge, Mass. $2.50. 195 pp. 1945.

This is one of those personal volumes concerning Freud by one of his earliest pupils. As such, it has a great deal of intimate material in it bearing on the character and work of Freud. These are days when books of this sort may be expected to multiply, and it is all to the good, since it will all help in the final evaluation of Freud as a man, as an artist, and as a scientist. This reviewer can only point with wonderment to the excessive degree of self-effacement, humility, almost of embarrassment which the author shows at inscribing his data. This remains unexplained, and since the book is about Freud and not about Sachs, maybe we have no right to insist on an explanation.

WENDELL MUNCIE

THE NEUROLOGIST'S POINT OF VIEW. *Essays on Psychiatric and Other Subjects.*

By I. S. Wechsler. L. B. Fischer, New York. $3.00. 251 pp. 1945.

This is one of those personal books in which the author, a noted neurologist, allows himself the privilege of discussing a great many things having little or nothing to do with neurology. In fact, the eleven chapters of this book have to do with various aspects of the racial psychology of the Jew and its bearing on the well known facts of nervous disorders among the Jews, the psychology of anti-Semitism, a sympathetic account of Zionism, together with observations of neurotic conflict from the psychoanalytic standpoint, a critical appreciation of Freud, a review of Moses and monotheism, a brief history of psychiatry, a rather defeatist chapter on the problem of mental disorders from the neurologist's point of view, and also one on the legend of the prevention of mental disorders.

Patently, these chapters are not all of the same importance from a scientific standpoint. I read hopefully the chapter, "Nervousness and the Jew; an Inquiry into Racial Psychology," in the hope of coming to a better grasp of this problem. I am not impressed with the author's argument that the Jew exhibits in a greater degree the struggle exhibited by everyone, that of conflict between reality and idealism. Also I feel fairly certain that even among Jews there are a great many people who would take issue with his statement that "a strong sense of reality alone would long ago have taught him (the Jew) the advantages of giving up his identity. It would long ago have convinced him of the egregious folly of being a Jew. But he could not yield his identity unless he consented to commit spiritual suicide. He could not, if he would, because his inner strivings, his ideal ego, stood sentinel over him. Those Jews whose greater sense of reality made them accept the advantages of non-Jewish life did so at the expense of their ideal ego and their cultural heritage."

In the chapter on "The Legend of the Prevention of Mental Diseases," the author makes some statements which need to be challenged. He says, "It is evident, therefore, that the ability to treat a disease, even to the point of cure, does not altogether depend on the knowledge of its cause, but it is absolutely certain that no diseases can be prevented unless its specific cause and the manner of its transmission are definitely known." As to this conclusion, it is almost certain that the old time syphilologist, who knew nothing about the specific cause and the manner of transmission of syphilis, knew enough to be able to teach that sexual continence was a practically sure preventive. Similarly he says, "There are diseases which we know neither how to prevent nor how to cure. . . .The same applies to most tumors of the brain, nearly all the psychoses, and a great many other conditions." This is palpably not the case, as any psychiatrist can avow. In the same chapter he launches a diatribe against psychiatry, accusing it of a "groveling worship of formulas, an infatuation with fetishes of words. New shibboleths are coined, and the illusion is created that new facts have been discovered. Abracadabra is uttered with the positiveness of magicians, and presto, new wisdom springs fullgrown out of nowhere. We solemnly speak of a psychobiologic or a psychodynamic approach, but if Socratically pressed for a real answer to the question: what is meant by psychobiologic or psychodynamic? we are in truth compelled to say, why—psychobiologic and psychodynamic." This is a serious charge and one which may be sustained only in part. It is true that there are people who do just that, but the great author of the terms psychobiology and psychodynamics as applied to psychiatry should be excepted from this general diatribe. If the author had undergone any serious training in psychobiologic or psychodynamic psychiatry, he would not be able to utter such bitter words. He would have realized that these are words not coined to cover up ignorance, but coined to furnish an incentive to discover more and more facts.

Already this review has given more attention to the book than it deserves. As stated in the first paragraph it is a personal document, and as such it is interesting. The author as a neurologist clearly has his limitations when he starts talking about things psychiatric. What he has to say is interesting and provocative, sometimes helpful and sometimes simply defeatist. All in all, it will repay reading.

WENDELL MUNCIE

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CONSCIENCE AND SOCIETY. *A Study of the Psychological Prerequisites of Law and Order.*

By Ranyard West. Emerson Books, Inc., New York. $3.00. 261 pp. 1945.

An American edition of the important book previously reviewed in this journal (vol. 19: 172. 1944).

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MIND EXPLORERS.

By John K. Winkler and Walter Bromberg. The World Publishing Company, Cleveland and New York. $1.00. 378 pp. 1939.

A reprint of the book previously reviewed in this journal (vol. 15: 260. 1939).

HUMAN BIOLOGY

THE SCIENCE OF MAN IN THE WORLD CRISIS.

Edited by Ralph Linton. Columbia University Press, New York. $4.00. xiv + 532 pp. 1945.

In his preface the editor calls attention to human inertia by stating that "it usually takes about a generation for the new discoveries and techniques of one science to become a part of the regular working equipment of other sciences. It takes considerably longer for such findings to become familiar to the layman and to exert any significant influence upon his thinking. The present book is an attempt to shorten this time interval." The rapidly growing science of man can and must be of aid in planning the new world order by showing the potentialities and limitations of the human material with which and for which the future is to be built. This collection of essays is not supposed to represent a condensation of all accumulated anthropological knowledge, but rather a report on recent advances in this science that deals only lightly with the facts and findings already well established. Thus, it is taken for granted that the reader "knows and accepts the basic facts of man's origin and evolution" and that he is fully aware of the issues of Negro and Jewish minorities. On the other hand, it discusses at length, e.g., the pressing problems of the American Indian, of which so few people are aware.

In the first chapter the editor presents authoritatively the Scope and Aims of Anthropology, which is defined simply as "the science of man and his works." Here it is pointed out that "anthropology has concentrated its interest upon a single organism, man, and has tried to understand all sorts of phenomena as they affect him." Thus it is a synthesizing science, split according to its definition, man and his works, into physical and cultural anthropology, aligned with the natural and the social sciences respectively.

The second contribution, entitled "Society and Biological Man," is by H. L. Shapiro. This brief review of the most significant biological facts relating to mankind deals with race-crossing, selection, environmental effects, etc., as far as general statements can be made to-day. This able, but necessarily fragmentary, outline of human biology demonstrates how incomplete our knowledge in this science still is, and how helpful it could be for the biological welfare of our populations.

The third paper, by W. M. Krogman, discusses that never-ending, controversial topic, "The Concept of Race." After emphasizing the fact that all men are far more alike than different, that all physical characters have a genetic basis, and that group differences exist chiefly in regard to the relative frequency of particular features, the author leaves no doubt of his conviction that differentiation has occurred and continues to occur in mankind. There follows a condensed presentation of the main physical characteristics of the three great human stocks, White, Yellow, and Black, and of the classification and probable interrelationships between the many minor groups. It is made clear that human races cannot be defined precisely and that "they are loose aggregates which precipitate out only en masse."

A further chapter, by O. Klineberg, on "Racial Psychology" leads to the blunt conclusion "that racial differences in psychology have not been—and perhaps cannot be—demonstrated." This, it appears, is largely due to the fact that no satisfactory tests of intelligence have as yet been devised which are entirely free of cultural or environmental influences.

Still another paper of great biological interest deals with "Population Problems." It is written by the botanist, K. Sax. Since this lucid contribution concerns itself with the latest and perhaps most consequential evolutionary specialization of man—the reliance on numbers of individuals—it deserves particularly to be widely read. Even though man has existed for a very long epoch, the world's population did not reach a one billion total until some time in the first half of the nineteenth century. In an additional one hundred years it nearly doubled, and in seventy years more it is expected to become doubled again. As the author states simply: "this. . .creates problems which lead to economic and military strife." He might have added that it cries for far-sighted social planning. Of the many interesting data in this chapter the following few examples may be quoted here: "During the past three hundred years the white population has increased about 700 per cent, the Yellow-Brown races a little more than 200 per cent, while the pure Negroid population has increased only about 100 per cent." No wonder that "of the people of European origin there are nearly half as many in other parts of the world as there are now in Europe." The author's comments and conclusions, though not new, cannot be stated too often, as they are rarely heeded. For instance: "Man has made little conscious effort to solve the problem of population growth and distribution." "If the birth rates are not restricted the population can be held in check only by a high death rate. This condition prevailed until modern times and still persists in most of Asia." "Control of the birth rate is essential in most parts of the world, and is prevalent in all countries which have attained a high standard of living." That the latter standard can become available to all seems most doubtful to the author in the present state of man's social evolution.

The sixteen remaining contributions to this volume are all devoted to cultural, social, economic, and political or administrative topics and as such are not to be reviewed in a biological journal, even though they are of great and timely interest to every one who shares the faith that the future of man has to be built on a Science of Man.

A. H. Schultz

A SCIENTIFIC THEORY OF CULTURE *and Other Essays. By Bronislaw Malinowski; preface by Huntington Cairns. University of North Carolina Press, Chapel Hill.* $3.00. ix + 228 pp. 1944.

Of the three posthumously published essays of the late Bronislaw Malinowski, who died three years ago at the age of 58, *A Scientific Theory of Culture* and *The Functional Theory* are almost identical in content, while the third, on Sir James George Frazer, containing personal memories and an analysis of Frazer's work from the functionalist point of view, transcends the scope of the preceding studies.

Malinowski is the outstanding representative of a whole period in anthropological thought which followed evolutionism and diffusionism, and which he called "functionalism." Mostly through his influence methods of field work have been greatly changed and improved, and a new approach to cultural anthropology has become predominant. Malinowski did not invent "functionalism," just as neither Marx discovered the "class struggle" nor Freud the "unconscious." But through his dynamic and rich personality, and a somewhat reckless and single-minded persistence, he has forced this principle upon his contemporaries, as Marx and Freud had done in their respective fields.

To Malinowski, the study of culture is the real meeting-ground of all branches of anthropology. Institutions are the legitimate isolates of cultural analysis, and are to be understood as culturally colored responses to a few basic biological needs. It is obvious that Malinowski's notion of function is closer to the biological than to the mathematical meaning of the term. His Functionalism is to a large extent the introduction of behaviorism into anthropology. Like behaviorism, it represents at once a great progress, and remains highly unsatisfactory as a total answer to the problem in question. It simply cannot be proved that every element of culture is functional in a biological sense, nor even that every element is functional at all. Functionalism which consciously omits every kind of historical reasoning is unable to explain the perplexing fact why the same basic biological needs receive such a multiplicity of answers in different cultures. That Malinowski eventually became aware of the latter problem can be seen in his third essay, where he tries to make a synthesis between his approach and the evolutionary and historical point of view.

It is impossible to go here into a detailed discussion of all of Malinowski's definitions, though probably more than the reviewer will be in definite disagreement with many of them, e.g., those given for "science," "politics," or "economics." In order to be just with the author, it is necessary to realize that not only his attempt at a general anthropological theory, but all similar attempts suffer from very serious shortcomings, and general anthropological theory is still in the stage of gestation. The relative absence of terminological acrobatics and the earnest search for the truth are very praiseworthy aspects of these essays. Though the posthumous publication of books has always seemed to me a highly problematic enterprise, it is on the other hand very practical to have Malinowski's theoretical system now available in a book, while heretofore it could only be found in his contributions to the Encyclopedia Britannica, the Encyclopedia of Social Sciences, and various articles and forewords. Malinowski had not fundamentally changed his point of view, when we compare these essays with the earlier ones, but he had become considerably more tolerant and inclined to incorporate the results of other schools and researchers. While he still did not find any place for physical anthropology in his system, the mellowness of age induced him to make even such extreme overstatements as, e.g., that Ellsworth Huntington had proved something "beyond doubt and cavil." The book is indispensable reading for all those who are interested in anthropological theory.

ERWIN H. ACKERKNECHT

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THE CULTURAL BACKGROUND OF PERSONALITY. *By Ralph Linton. D. Appleton-Century Company, New York and London.* $1.50. xix + 157 pp. 1945.

Studies on the relations of personality and culture have brought about closer collaboration between anthropologists, sociologists, and psychologists. Ralph Linton of Columbia University, who has been one of the pioneers of these cooperative efforts, and who has consistently dealt with different aspects of the problem in his earlier books, sketches a conceptual framework for the systematic study of culture, society, and personality in this little volume, based on five lectures delivered at Swarthmore College in 1943.

In the study of culture Linton has introduced the useful differentiation between overt and covert aspects of culture, and between real culture, the culture construct, and the ideal pattern of a culture. In the analysis of social structure, he emphasizes the notions of status and role. As to personality, the responses forming it are divided into specific and general ones. The latter are highly dependent on the value-attitude systems of the individual. Though biological factors undoubtedly contribute in the formation of personality, especially in small, isolated, intermarrying communities, personality is mainly formed by culture in the process of child rearing, and by being provided throughout life with new cultural models for specific responses.

The author has been strongly influenced by behavioristic methods, but largely transcends this rather limited approach, as, e.g., in his excellent statements on psychic needs and the double role of the individual as object and subject of society. In spite of the somewhat algebraic character of the small book, which makes it sometimes no easy reading, it will undoubtedly be highly appreciated by all interested in the problems of culture and personality for its lucid analysis and highly stimulating qualities.

Erwin H. Ackerknecht

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The Hopi Way.

By Laura Thompson and Alice Joseph. Foreword By John Collier. University of Chicago Press, Chicago. $3.00. 151 pp., 24 plates. 1944.

This is a work done in cooperation between the Indian service and the Committee on Human Development of the University of Chicago. Its purpose is to get behind an Indian way of life; to try to avoid our preconceived ideas about "the Indian," and to try to find what individuals within a group are like, and thereby to gain some idea of how the group functions. From this base it is the hope of the Indian Service to build better administrative programs aimed at doing the maximum good for the tribes and the minimum harm.

The work is intended to be holistic in its approach. The natural environment, economy, history, and social structure of the group, as well as the life cycle of the individual is presented. The major emphasis falls on the analysis of the psychological tests given the Hopi children (Rorschach, Thematic Apperception, and six others). A series of selected individual analyses are presented to illustrate different types of adjustment within the Hopi social group.

The work tends to show a very well adjusted group of peoples existing in a difficult natural environment and maintaining nearly intact their ancient social culture. It is an excellent study. If any critical comment were called for, it would merely be that the lengthy testing had brought to light disproportionately few new insights into Hopi culture. In the sharpening of our understanding, however, it is a considerable contribution. Psychologists should be particularly interested.

George F. Carter

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The Aleutian Islands: Their People and Natural History (*With Keys for the Identification of the Birds and Plants*). *Smithsonian Institution War Background Studies Number Twenty-one.*

By Henry B. Collins, Jr., Austin H. Clark, and Egbert H. Walker. Smithsonian Institution, Washington. 25 cents (paper). iv + 131 pp.; 21 plates. 1945.

This is a brief presentation of the history, ethnology, and natural history of the Aleutian Islands. It is aimed primarily at the service men stationed there and is designed to aid them in getting to know the area.

The introductory section on "The Islands and Their People" is compact and interestingly written. There is a description of the geography and a good accompanying map. The history of the discovery and exploitation of the islands is given. The sketch of the people is brief and avoids technical details that the non-anthropologist would struggle over.

The section on "Animal Life of the Aleutian Islands" stresses the rich bird life of the area. The fishes and sea mammals are also described. Appendices give a list of common mammals, common birds, and a key to the recognition of the birds of the area.

The third section, "Plants of the Aleutian Islands," sketches the plant life found there. It is supplemented by appendices listing the plants, and giving a key to the recognition of the plants of the islands.

George F. Carter

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Europe: *An Atlas of Human Geography.*

By Marthe Rajchman. William Morrow and Company, New York. $2.00. 120 pp. 1944.

This is a book of maps, charts, graphs, and diagrams assembled with the aim of providing background for understanding the problems of Europe. The data and the maps have been culled from a variety of sources. The assemblage of maps is useful for gaining a quick view of some aspects of Europe. A great variety of subjects, from simplified climates and linguistic and national distributions to national income and wartime population movements are shown.

There is an accompanying text which is neither very convincing as to the author's geographic expertness nor very significant. It does not seem correct to call Europe the densest human agglomeration in the world; *global* connections with Europe should surely consider more than the North Atlantic routes to Europe; few will believe that Europe has the best climate in the world for human activities; etc.

George F. Carter

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Food, War and the Future.

By E. Parmalee Prentice. Harper and Brothers, New York and London. $2.50. xii + 164 pp.; 5 plates. 1944.

The author of *Food, War and the Future* writes with an abundance of literary references in a style of considerable charm. He attacks with vehemence and defends with ability. His first chapter raises the specters of a world population increasing in unlimited fashion, of want returning, of the tide of yellow Asia rolling over the western continents. With neo-Malthusian enthusiasm he discusses the recent "Century of Grace" the West has had, in its relative freedom from want, for the first time on a large scale in human history. The predictions of returning disaster, however, seem to be based on the assumption of constant rates of increase in population and to ignore the sounder and more conservative demographic estimates to be found, for example, in such studies as those in *World Population in Transition*, reviewed elsewhere in this issue.

Prentice places his hope for future freedom from want on the achievements of genetics applied to plant and animal breeding. At this point we meet another of the author's *bêtes noires*—the prevailing regard for pedigreed pure-bred stock in the improvement of dairy cattle. He demolishes the myth of the early foundation of the well-known breeds, and is devastating in his criticism of the professors in agricultural colleges who have taught and endorsed these historical fairy tales. He does the pure breeds an injustice, however, in failing to cite the data that show how much of an improvement in milk production has actually accompanied the development of the pure breeds. He is perfectly right, of course, in emphasizing the complete superiority of the progeny test as a measure of breeding worth.

Prentice next proceeds to discuss the relation of human freedom to want, under the heading of "Democracy in America." Here he reveals his basic point of view more clearly. It is that of the nineteenth century liberal transmuted into laissez-faire individualist and isolationist. The transition is subtle. "American democracy is found in the inalienable and equal rights secured to all persons by the constitution." "There can be no freedom and no democracy without effective limitation upon government, and government is no friend to limitations upon its power." "It is very disturbing, indeed. . .alarming, to think of the sudden rise in Great Britain and America of the demand for a protected life." "No government is productive." "At the worst America can not be defeated. Without American supplies. . .Great Britain is helpless, but America would be stronger than ever were she to withdraw from Europe and hold her own frontiers free from the burden of defending other nations." "The Beveridge plan is at best a temporary expedient. It is not a living system under which society can endure." He speaks approvingly of German rule over central Europe as the best ultimate solution of the European problem. "The freedom we intend to preserve is the constitutional freedom which brought the American era, nothing less and nothing different"—and therefore nothing more!

This is a most interesting book, stimulating in many respects—this must be said in spite of one's severe criticism and perhaps fundamental disagreement as to ultimate conclusions.

BENTLEY GLASS

WORLD POPULATION IN TRANSITION. *Annals of the American Academy of Political and Social Science, Volume 237, January, 1945.*

Edited by Kingsley Davis. The American Academy of Political and Social Science, Philadelphia. $2.50 (cloth); $2.00 (paper). viii + 257 pp. 1945.

No more comprehensive and varied a survey of world demographic problems could be wished at the present time than this special number of *The Annals*. It begins with a general article by the editor on "The World Demographic Transition." There follows a section of regional studies, on the United States (Philip M. Hauser and C. Taeuber), South America (Halbert L. Dunn, Hope T. Eldridge, and Nora P. Powell), Central and Caribbean America (Alberto P. León and Alvaro Aldama C.), postwar Europe (Dudley Kirk), Russia (M. Kantorovitz Gordon), Japan (Irene Taeuber and Edwin Beal), China and southeastern Asia (Warren Thompson), the British Dominions overseas (Enid Charles), the Mohammedan world (Ernest Jurkat and Louise Kiser), and primitive areas (S. F. Cook). The second section deals with various aspects or factors of population change, and contains: Trends, Determinants, and Control in Human Fertility, by P. K. Whelpton and Clyde Kiser; Trends in Longevity, by Louis I. Dublin and Alfred Lotka; Infant and Maternal Mortality in the Modern World, by Jacob Yerushalmy; The Trend Toward an Older Population, by John Durand; Sickness and Health—Their Measurement, Distribution, and Changes, by Selwyn Collins; Pressures and Barriers in Future Migration, by Edward Hutchinson and Wilbert Moore; Relocation of Europeans, by Imre Ferenczi; Population and Per Capita Income, by Joseph Spengler.

The volume ends with an excellent summary of the Issues of Population Policy, by Frank Lorimer. Not only every biologist, but every alert citizen is urged to study this collection of papers thoroughly. No intelligent understanding of world affairs can fail to take into account the problems it discusses.

BENTLEY GLASS

BIOMETRY

EINFÜHRUNG IN DIE WAHRSCHEINLICHKEITSTHEORIE. *By Erich Kamke. (S. Hirzel, Leipzig); J. W. Edwards, Ann Arbor, Michigan.* $3.85. vii + 182 pp. (1932); 1944.

The publication of an American edition of this book is under the authority of the Alien Property Custodian. The book is not a translation but is a lithoprinting of the original edition.

The author refers in the foreword to the increased importance of probability theory to scientists, because of the recognition by modern physicists of its role in their science. He undoubtedly has this group in mind in his presentation.

The probability of an event, according to Kamke's concept, is the limit of the ratio of the number of occurrences of the event to the number of trials, as the number of trials is increased indefinitely. The book presents under this definition the classical theory of the fundamental theorems of addition and multiplication and some of the famous problems on games of chance in Part I, and then takes up errors of observation, the Bernoulli and Lexis theories, and the normal curve in Part II.

The definition of probability as the limit of the relative frequencies in this presentation is that of Von Mises and certain other recent writers on probability. Although it is desirable to have inaccessible foreign publications made available, this particular one adds so little that is new that one might well question the importance of publishing it under the circumstances involved in the copyright situation during the war.

MARGARET MERRELL

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STATISTICAL METHODS FOR RESEARCH WORKERS. *Ninth Edition, Revised and Enlarged.*
By R. A. Fisher. Oliver and Boyd, Edinburgh. 16s. xv + 350 pp. 1944.

Except for minor changes, this is the same work that has long since become standard in its field in earlier editions (see review in this journal, vol 17: 189. 1942). A new section (57.3) has been added on the testing of homogeneity of evidence used in estimation.

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DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

LABORATORY METHODS OF THE UNITED STATES ARMY. *Fifth Edition.*
Edited by James Stevens Simmons and Cleon J. Gentzkow. Lea and Febiger, Philadelphia. $7.50. 823 pp.; 8 plates. 1944.

The well printed, well bound fifth edition of this manual was prepared—like the first edition, which appeared during World War I—to describe "practical methods for use in the medical and sanitary laboratories of the Army." More specifically, it was designed "for the large numbers of officers and technicians who entered the Army and assumed responsibility for its enormously expanded laboratory services." Sufficient theory is included in its more than eight hundred pages to make possible intelligent and even versatile work. This manual does not claim to have everything about everything, but the material covered is so extensive that it is difficult to imagine any kind of a biological laboratory in which it would not be an extremely valuable reference.

Part I—Clinical Pathology, includes twelve chapters ranging from Kidney Function Tests and Hormonal Tests for Pregnancy to chapters on Human Blood Groups and the Diagnosis of Syphilis. Part II—Chemistry, with eight chapters, runs from General Chemical Technic and Blood Chemistry to Toxicological Methods and Useful Recipes. Part III—Mycology. Part IV—Bacteriology, includes chapters on General Technic, Classification, Bacteria of Medical Importance, Bacteriologic Examination of Milk, Water and Sewage. The remaining seven portions of the manual cover respectively, Part V—Rickettsiae and Filtrable Viruses, Part VI—Protozoology, Part VII—Helminthology, Part VIII—Entomology, Part IX—Pathology, Part X—Veterinary Laboratory Method and Part XI—Statistical Methods.

In general, the twenty-six contributors have turned out a remarkably competent and up-to-date piece of work. As a rule the explanations are clear, the directions adequate and specific. The range of material is such that it will be of practical use both to the architect turned medical corpsman and to the veteran of the laboratory or the specialist with three degrees after his name.

Any manual bearing the proud title of this one should be second to none. The urgency of the need is too great to tolerate either lack of adequacy or second-best methods. Obviously, no one individual is competent to judge every section of a volume of this scope. Nevertheless, anyone with even a moderate amount of laboratory experience cannot fail to be distressed at the evidences of either haste in preparation or lack of experience in writing directions that are to be followed by men or women working on their own. Examples are to be found in several parts of the book.

The section on medical entomology, admirable in most respects, unaccountably recommends a compound microscope for use in the identification of insects, when a binocular dissecting microscope is many times superior. The keys could be improved. The first bedbug brought in for identification (surely not an unlikely contingency) will stall early in the first key. The key for the fleas depends on technical terms not always explained. The figures of fleas could both be improved in clarity and made more relevant. The several pages discussing families and genera of insects of medical interest are rendered worthless from any practical point of view by a lack of figures, keys, or diagnostic descriptions. Sergeants may be grateful to learn that the Anthomyiidae includes, *inter alia*, the "latrine fly," *Fannia scalaris*, but there is nothing in this manual that would enable a full colonel to recognize one when he saw it.

The directions for the diagnosis of rabies in a dog are unnecessary if the technician already knows how, inadequate if he does not. These directions call for staining parts of the hippocampus major for Negri bodies. Detailed instructions are given for preparing and using both Seller's and Mann's stains. But what is the unfortunate man to do who has forgotten what and where the hippocampus major is? There is neither a diagram nor a description of it. Neither is there a figure or description of a Negri body. It would seem desirable to enlarge on the bare statement that Negri bodies should appear red, and to include, as many manuals do, a word of caution about the need for wearing rubber gloves and even goggles in handling the head and removing the brain of a dog suspected of being rabid.

The Arneth leucocyte count and Schilling's modification of it are discussed at some length, but without either diagrams or definite percentages, so that from what is given here it would not be possible to make such a count. Directions are given for removing various stains from clothing, including blood stains, but we fail to find any mention of serological tests to determine whether or not such a stain was made by human blood—sometimes a question of great importance. Directions for embalming are given with a wealth of detail that would have delighted Edgar Allen Poe. Everything is there,—everything, that is, except the formula for embalming fluid. (This is no professional secret, as the formula approved by the American Funeral Director's Association is published in the Scientific American Cyclopedia of Formulas.) The bacteriological standards for the purity of milk are incompletely given. The standards for cream are so vague they are virtually meaningless. The section on the fungi seems curtailed. The section on the microscopic study of tissues has no instruction for one of the trickiest and most necessary of laboratory chores, sharpening a microtome knife.

In short, notwithstanding all the virtues of this manual, and they are many, there are good reasons for hoping that no one will have to wait a decade for the next edition, as we did for this one. A sixth edition, remedying the deficiencies of the present volume and incorporating the results of experience with DDT and all the other new materials and new methods, would win universal acclaim.

GAIRDNER MOMENT

* * *

SEEING THE INVISIBLE. *The Story of the Electron Microscope.*

By Gessner G. Hawley. Alfred A. Knopf, New York.
$2.50. xv + 195 + ix pp. 1945.

Here is a book written in a simple, almost elementary style that succeeds in making clear the principles of operation of the electron microscope, its powers, and its disabilities, especially in dealing with biological objects. The history of the instrument is recounted, and its achievements to date are amply illustrated. The author commits a few gross biological errors, attributing the action of serums and vaccines to bacteriophages, for example, and confusing photosynthesis with protein synthesis. It is amusing to read that genes are carried in "red-colored rod-shaped envelopes in the sex cells." But on the whole, the account is good, and should be intelligible to anyone with enough intellectual curiosity to pick up and read a book about the electron microscope. The outstanding value of the book consists in its abundant and well reproduced illustrations. For these alone most biologists will want to own *Seeing the Invisible.*

ERRATUM

In the June number of THE QUARTERLY REVIEW OF BIOLOGY (page 186), the price of the Bulletin of the National Research Council Number 109, "Inadequate Diets and Nutritional Deficiencies in the United States," is incorrectly stated. The price is 50 cents.

JOHN CAMPBELL MERRIAM

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THE PROBLEM OF CENTRAL NERVOUS REORGANIZATION AFTER NERVE REGENERATION AND MUSCLE TRANSPOSITION

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INTRODUCTION

If the regeneration of nerve fibers after peripheral nerve lesions regularly restored in perfect detail the original connections between the central nervous system and its end-organs, nerve regeneration would not present a problem of central nervous reorganization. To attain such perfect regeneration it would be necessary that each one of the hundreds of fibers of various types in the proximal nerve stump be guided into its own original channel in the distal stump and hence out to its proper end-organ in the periphery. However, such perfect guidance of regenerating fibers back to their appropriate terminations is, of course, never achieved or even approximated after nerve section. Misdirection of the outgrowing fibers, resulting in their loss and in their haphazard redistribution to foreign end-organs, has long been recognized as a conspicuous feature of nerve regeneration (Langley, 1918; Cajal, 1928; Weiss, 1937a; Young, 1942). If normal smooth function is to be restored to the reinnervated parts, extensive central nervous readjustments must therefore take place.

The following list of factors all tending to cause distortion of the normal innervation pattern following nerve lesions indicates the nature and extent of the readjustment problems with which the centers must cope. (1) The outgrowth of fibers from the proximal nerve stump and their entrance into the neurilemmal tubes of the distal stump is apparently non-selective, with no biochemical attractions or affinities of individual fibers for their original pathways. The motor fibers of a flexor muscle, for example, may become scattered fortuitously into various foreign channels leading to extensor, pronator, supinator or any other skeletal muscles or autonomic effectors supplied by the severed nerve. Motor fibers may also be misdirected into sensory channels. As far as is known, any regenerating fiber of a severed nerve may enter and grow distally within neurilemmal tubes previously occupied by any other fiber, or between such tubes. (2) The direction of outgrowth of fibers across the gap between the nerve stumps is dependent upon submicroscopic mechanical factors which are very easily disturbed, causing deflection of the fibers from a straight course. Assuming that the nerve ends have been neatly apposed in correct orientation, any of the following or similar factors may cause gross deflection of fibers into foreign pathways: (a) local foci of infection; (b) irritative foreign bodies, such as suture materials; (c) scar formation; (d) irregular tension and pressures, or simply absence of straight longitudinal tension on the substrate between the nerve ends. (3) Regenerating fibers show a tendency to undergo multiple branching in the scar region, so that single fibers become connected with several end-organs, which may all be of different function. (4) With the common methods of suture many fibers become lost in local neuromas, in Perroncito coils, and in scar tissue around the point of union. Also, a varying percentage of fibers fail to enter tubes of the distal stump and instead grow distally between the tubes. Such inter-tubal fibers must often become lost or take an abnormal course in the periphery. (5) Regenerating nerve fibers are of much smaller diameter than mature fibers, with the result that as many as ten or more regenerating fibers often enter a single tube formerly occupied by only one axon, leaving pathways to other end-organs completely uninnervated. (6) The extreme microscopic precision required in the apposition and orientation of the nerve ends to assure an accurate spanning of the nerve gap is only a hypothetical ideal which remains utterly unattainable in practice. Recent advancements in nerve splicing methods (Weiss, 1943a, b) promise to reduce the multiple branching, loss of fibers, and tortuous outgrowth across the nerve gap; but even if perfectly straight outgrowth across the gap could be obtained, it would result in normal innervation only if the cross sections of the two nerve stumps were aligned with microscopic exactness. The best methods of nerve splicing when applied under optimal conditions can be expected to yield at most only a statistical predominance of appropriate over inappropriate nerve fiber connections. (7) In clinical surgery, conditions frequently make it impossible even to attempt any accuracy in orienting and aligning the cut faces of the nerve stumps. Accidental lesions are rarely clean transections which permit neat reunion of the nerve ends. In delayed sutures, scar formation often obscures beyond recognition the original orientation of the nerve stumps, leaving their alignment at secondary apposition largely a matter of chance. Resection of fibrotic nerve ends is usually necessary in such cases. If intraneural plexuses (Langley and Hashimoto, 1917) are present in the excised stretch of nerve, then accurate apposition even of fascicles will be impossible, even though the general orientation of the nerve may still be discernible. (8) Frequently the gap between the nerve ends is so large that direct reunion of the nerve with the limb in normal position is impossible. Recent evidence (Highet and Sanders, 1943; Weiss and Taylor, 1943a; Weiss, 1943c) indicates that the use of grafts to bridge such large gaps may be more favorable for nerve regeneration than the extreme manipulative measures favored in the past. The presence of grafts or other types of bridge spanning the gap must necessarily greatly enhance abnormal redistribution of regenerating fibers. Internal nerve plexuses in the nerve graft or in the excised portion of the nerve will cause additional distortion of the normal innervation pattern.

Thus, in summary, the nature of nerve outgrowth, limitations in nerve splicing methods, and unavoidable obstacles inherent in accidental nerve injuries, all tend to preclude any perfect restoration of peripheral nerve linkages. Distortion of the normal innervation pattern is always in some degree inevitable and, particularly in clinical practice, a completely haphazard reshuffling of relations between the central nervous system and the end-organs supplied by the divided nerve is often unavoidable. The disarrangement will be the greater, the larger the nerve trunk involved and the more heterogeneous the function of its constituent fibers and end-organs.

Even more abnormal are the terminal connections resulting from nerve crossing, i.e., the union of the central stump of one nerve to the distal stump of another. Although employed more liberally in experimental studies, nerve crossing is not uncommon in clinical surgery in cases where it is impossible to use the central stump of the damaged nerve (Stookey, 1922; Pollock and Davis, 1933). Nerve crossing deliberately forces all the regenerating fibers to terminate in foreign end-organs, which may be far removed both in anatomical location and in mode of function from the nerve's original endings. In addition to this wholesale switching of nerve fibers from one region to another, nerve crossing involves also, like reunion of the ends of the same nerve, a disorderly redistribution of individual fibers within the nerve itself. This internal reassortment of fibers of different function within the reinnervated area is worse after nerve crossing than after direct reunion, because there usually is no correspondence whatever between the intraneural fiber pattern of the distal stump and that of the central stump. The outmoded method of lateral implantation and the crushing and severance methods (Kilvington, 1905; Dogliotti, 1935; Aird and Naffziger, 1939; Billig and van Harreveld, 1943) for utilizing the excess branches of regenerating fibers to supply an extra load of end-organs also deliberately foster confusion in the innervation pattern.

To what extent, if any, can central nervous reorganization compensate for, and correct, the sensory and motor dysfunction which otherwise must inevitably follow such rearrangements of peripheral nerve connections? Compared to the surgical problems, histological aspects, and immediate physiological results of the treatment of peripheral nerve lesions, the qualitative problems of functional recovery raised by the shunting and crossing of nerve fibers have been largely neglected. On the motor side, the problem is that of readjusting the timing and rate of discharge of misdirected motoneurons. On the sensory side, the problem is one of altering in accordance with their new end-organs the central sensation and response associations of the misdirected afferent fibers. This problem of recovery of function in natural systemic activities is to be distinguished sharply from the mere re-establishment of transmission of excitation from nerve to end-organ or vice versa, recovery of muscle volume and contractility, quantitative recovery of general sensibility, etc. Thorburn (1920a) has justly contrasted mere physiological success with what he called the "economic" success of nerve regeneration. More recently Sanders and Young (1942) and others have stressed our present lack of knowledge regarding the qualitative aspects of recovery and the importance of giving them more heed in the future. The general lack of reliable information regarding the functional results of misdirection of nerve fibers in regeneration is becoming recognized as a definite handicap to more rapid progress in the treatment of peripheral nerve lesions.

The present survey does not devote any primary consideration to those functional recoveries effected through compensatory adjustments in the remaining intact or sound parts of the organism. Just as it is possible to compensate to some extent in various performances for the complete loss of a limb, so it is possible to compensate for paralysis or dysfunction of a limb or its parts. The underlying central nervous reorganization involved in such compensatory readjustments in the sound parts of the system is of a more common and simple type than that generally required to readapt directly the function of the disarranged nerves and end-organs. Also such compensatory adjustments at their best cannot be expected to approximate the optimum recovery which would be achieved by complete restoration of adaptive function to the affected nerves and end-organs themselves. Whether or not the abnormally innervated or transposed end-organs can themselves come to function again in a proper adaptive manner as a result of central nervous reorganization poses at present the primary and more fundamental problem, from both the practical and theoretical viewpoints. It is this aspect of recovery with which the present review is specifically concerned.

Previously, this problem has received attention largely for its bearing on theoretical questions pertaining to such subjects as central nervous plasticity and adaptability, anatomical localization of central readjustments, equipotentiality vs. specificity of central reflex associations, peripheral vs. central control of coordination, innate vs. acquired nature of central and peripheral relations, selectivity of nerve regeneration and termination, the manner of ontogenetic development of connections between center and periphery, and related topics. The problem also has immediate practical significance in the treatment and handling of peripheral nerve injuries and paralyses of different kinds; for example, in the choice of surgical methods and procedure, in determining the possibilities and limitations of functional repair by muscle and nerve substitutions, in constructing reeducation and rehabilitation programs, in evaluating compensations for disability, and wherever prognosis of the quality of functional recovery is important.

Previous views and conclusions

In the past an overwhelming majority have concluded that complete recovery of normal function after nerve crossing and regeneration as well as after muscle transposition is definitely possible and regularly occurs not only in man but in the lower mammals as well. The most extensive review of the subject is that by Bethe and Fischer in 1931. After summarizing all the available studies, they emphasize with italics the conclusion that there can be no doubt from the existing evidence that the nervous system can adjust fully and completely to changes in the anatomical connections brought about by nerve interchanges. They conclude that not only correct motor coordination, but also correct sensory localization is usually recovered after peripheral nerve exchanges in other animals as well as in man. From the rapidity of the restoration of correct function reported frequently to follow nerve crossing and muscle transplantation, they deduce further that central nervous integrative processes are conditioned much more by peripheral connections than by connections in the central organ itself.

Anokhin and his collaborators have devoted many years to the study of the functional results of nerve regeneration and interchange of peripheral nerve connections. In their monograph (1935a) they maintain that they have demonstrated that organs which have been supplied with an unusual innervation do acquire in the end their regular function. They believe that the normal distribution of nervous impulses in the centers is not at all rigid and unchangeable but very mobile, and even at the spinal level is capable of complete adaptive reintegration after alteration of the phylogenetic connections between central nervous system and periphery. Later (1940), Anokhin again asserts, on the basis of the results of nerve crossing, that the specificity of the spinal motor centers is not fixed and constant but depends upon the connections with peripheral organs.

Foerster (1930), after long clinical experience with recoveries from nerve injuries and after clearly schematizing in some detail the extensive shifts in central nervous associations from the cortex to the spinal centers that are necessary for recovery after nerve crossing as well as after straight reunion, states that recovery nevertheless occurs and that the new relationships that have to be formed in the centers come eventually to function as well as did the pre-existing normal relations.

Stopford (1930), as did Osborne earlier (1909), assumed that reeducation is possible after misdirection of sensory nerve fibers and explained the delay in reappearance of so-called "epicritic" sensation after nerve regeneration on the basis of a reeducation period in which the higher brain centers are adjusted to the new afferent terminations.

Lee, in his 1929 review of nerve regeneration, described the aberrant outgrowth of nerve fibers and after pointing out that, due to shunting in the scar region, every end-to-end nerve suture is really an example of multiple cross unions, he concluded with the assumption that reeducation within the central nervous system probably smooths out the dysfunction produced by these wholesale anatomical aberrations.

Perthes (1922), in his review of functional recovery after nerve injuries of the first World War, introduced his discussion with the statement that experimental nerve reunion in animals leads with certainty to complete recovery. He also emphasized the extreme suddenness with which readjustment may occur in human patients after abnormal reinnervation as well as after muscle transposition (Perthes, 1918), and referred to the rapid learning of the brain to adjust to the new anatomical relations.

Kennedy published, with thorough reviews of the earlier literature, a number of extensive experimental and clinical observations over a period of 20 years beginning in 1897, on the problem of central readjustment after nerve regeneration. He remained strongly convinced on the basis of the experimental and clinical data that normal function, both motor and sensory, is restored following the cross union of peripheral nerves as well as after their straight reunion. In one of his last reports (1919) he listed a number of clinical cases in which, after complete severance of nerve trunks of the arm, sensation and motion were restored so as to give restoration of normal function. He said further that recovery after complete division of nerves was not different from that after simple compression, which latter causes interruption of nerve fibers but does not lead to disarrangement of the innervation pattern. Kennedy's views and experiments have frequently been cited in the clinical literature as evidence that reeducation may effect complete recovery following abnormal reinnervation.

Spitzy (1908), after considerable study of functional recovery after nerve crossing, both experimental and clinical, and with some appreciation of the complications involved in compensating for the anatomical confusion inevitably wrought by nerve crossing, was moved, in describing successful recovery in some of his patients, to refer enthusiastically to the "wunderbare Selbstregulierung" and "kolossalen Anpassungsfähigkeit unseres Nervensystems."

Of the even more numerous reports of good functional recovery after muscle transposition, those by Marina (1912, 1915) are outstanding. He concluded on the basis of the results of muscle transposition in man, and particularly on the basis of his experiments on reciprocal antagonistic transposition of ocular muscles in the monkey, that the functions of central association pathways and intranuclear connections of the brain and cord are not rigidly specialized, as traditionally assumed, but are entirely plastic and dynamically regulated. He made a strong plea for a complete revision of our central nervous physiology from the ground up, to bring it into accord with the extreme dynamic adaptability which he had observed.

The above reports and generalizations are a few among many which would endow the central nervous system with special and very remarkable capacities for maintaining functional proficiency in the presence of the extreme anatomical chaos that follows nerve crossing and regeneration and the less drastic disarrangements of muscle transposition. In view of the existing literature, Goldstein (1939) was not unjustified in his discussion of the problem in stating that such central nervous reorganization occurs very readily, often spontaneously without any training. He believed that the evidence fully supported his contention that it is immaterial what particular nerve fiber connections exist between center and periphery; that so long as any connections whatsoever are present, correct function follows. The practical as well as theoretical import of such conclusions as the above is obvious. Even such a practice as dissecting out full length the healthy ulnar nerve of the arm and crossing it to the leg nerves to restore function to the lower limbs of patients paralyzed by cord transection, as undertaken by Krukenberg (1918), might be considered justified by the earlier literature.

Although these views have long prevailed, their acceptance has not been entirely unanimous. Occasional dissenting opinions and objections are to be found scattered through the literature. Recently, on the basis of clinical evidence, Ford and Woodhall (1938) have questioned quite strongly the prevalent assumption that reeducation may compensate for misregeneration. Moreover, within recent years a number of controlled mammalian experiments designed to further analyze central nervous adaptation to disarrangement of the normal relations between center and periphery (Sperry, 1940-1943) have yielded results in direct contradiction to the optimistic views cited above. Instead of complete rapid reorganization to suit new peripheral relations, nerve-muscle rearrangements were found to result in intractable perverse discoordinations and maladaptive reversals of response which in most cases persisted indefinitely with no sign of correction. Results equally clear obtained in amphibians (Weiss, 1941c; Sperry, 1943a-1944) have also proven irreconcilable with the contentions of Bethe, Anokhin, Goldstein, Marina and their followers regarding the basic placticity of the vertebrate nervous system and the absence of any fixed functional specificity in the linkages between center and periphery and between and within nuclei of the cord and brain.

The recent contradictions, in conjunction with other scattered reports of persistent malfunction particularly following nerve redistribution, cast doubt upon the long prevalent generalizations and indicate that the problem is by no means satisfactorily settled. Critical reexamination of the evidence and a thorough reconsideration of the entire question is particularly urgent at the present time because of the large number of cases of peripheral nerve lesions coming in for treatment, the consequent impetus to research on related phases of nerve regeneration, and increased opportunities for further study of the late, qualitative aspects of recovery. Because of the controversial status of the problem and because the material has not previously been collected and adequately summarized, a fairly extensive survey is offered. Rather than to attempt to draw any definite conclusions, the main purpose of the present paper is to gather and review critically the bulk of the widely scattered reports bearing on the subject.

EFFECTS OF INTERCHANGING MOTOR NERVES

Although there is a tremendous literature on the results of surgical reunion and crossing of nerves, the major portion of it is of no consequence to the problem of central nervous readaptation, because the qualitative aspects of recovery were not considered and no pertinent data were recorded. It will become clear that most of the evidence, both clinical and experimental, has been drawn in the past from cases of nerve crossing rather than from cases of straight reunion, even though, as mentioned above, every case of nerve reunion is actually a case of multiple cross-unions of different fiber types within the nerve trunk. The reasons are several. First, after crossing nerves, all fibers are directed to foreign end-organs. After reunion of the ends of the same nerve, on the other hand, there is always a probability that a certain percentage of fibers have returned to their original end-organs, leaving it doubtful how much of the recovery of normal function is due to correct regeneration and how much to central adjustment. Second, determination of the quality of motor or sensory recovery is usually at best difficult. Crossing nerves of widely different function whose terminations are well separated leads to a functional result that is much more easily detected and evaluated than are the more subtle defects that follow straight reunion of a single nerve. Third, after straight reunion, the multiple branching of single fibers to several end-organs, often of diverse function, may permanently prevent any dissociation in the function of these end-organs. It may thus be doubtful after straight reunion whether persisting association of movements or sensation is due to lack of central plasticity or to excess branching of single fibers. After successful end-to-end nerve crossing, by contrast, single fibers are not able to send branches to both the original group of end-organs plus the new group, so that any persisting functional association between the new and old regions supplied by the crossed nerve cannot be blamed on fiber bifurcation. For these reasons most of the experimental, and also the most decisive clinical evidence, has been derived from cases of nerve crossing rather than of straight reunion.

Although regeneration of most peripheral nerves presents a problem both of sensory and motor recovery, and although the readjustment process itself may necessarily involve inseparable sensory-motor mechanisms, the evidence related to misdirection of motor fibers on the one hand, and of sensory fibers on the other, is here separated for convenience of discussion.

Flourens' Classic Experiment

It is generally agreed that the first attempt to study the results of crossing nerves was made by Flourens (1828). In a cock, he cut and crossed the two main nerves leading from the brachial plexus to the ventral and dorsal aspects of the wing, respectively, and reported that after a few months the bird recovered use of the wing so that it could fly as well as before. This first, classical experiment has been repeatedly cited over since as an example of the recovery of coordinated action after switching the innervation of antagonistic muscles.

In considering the recovery of flight in this case, it must be remembered that the main muscles of flight acting on the humerus of the wing were not affected by the operation. It is probable that the muscles acting on the elbow joint of the wing also retained their complete normal innervation, for they are supplied by small nerve twigs high under the shoulder, and furthermore, Flourens himself indicates that his operation affected only the extremity of the wing. The tensor muscles of the patigial membrane of the wing were also probably not cut in the operation, according to Cunningham (1898), who suggests that these muscles, rather than the test muscles, may have been primarily responsible for the recovery. Flourens failed to give a detailed description, but it thus appears very probable that only the small muscles acting on the carpal joint of the wing were affected by the operation.

The action of the carpal joint of the wing in the flight of the domestic cock is not a very delicate indicator of the differential reciprocal function of antagonistic muscles. With normal action of the proximal joints, a simple sustained rigidity of the carpal joint would be sufficient to give to most observers the impression of normal flight. Moreover, the ligaments and tendons of the cock's wing are such that extension of the elbow joint, as in flight, secondarily produces a full extension of the terminal wing segment accompanied by a firm spreading of the large distal wing feathers. Flexion at the elbow releases this passive extension of the carpal joint and permits carpal flexion. With this secondary distal action of the elbow muscles, plus the direct action of the elbow muscles and also of the main flight muscles of the shoulder and finally of the patigial tensors all remaining intact, it is not surprising that good use of the wing was recovered.

Stefani (1886) mentions in regard to Flourens' experiment that the normal flight of the pigeon is not noticeably affected by cutting either one of the two main nerves of the wing. Drooping of the distal wing segment is the most obvious defect that would be anticipated after Flourens' operation. It is quite possible that nerve regeneration bringing return of muscle tonus and contractility and perhaps also contracture would remedy this defect and at the same time restore sufficient rigidity to the extended joint to greatly improve its use in flight without any reorganization of central nervous coordination. Schiff (1885) has pointed out that Flourens' description was too short to give any indication as to whether the action of the reinnervated muscles was actually coordinated or not. Cunningham (1898) questioned the purity of the crossed regeneration, suggesting that stray fibers may have reentered their original distal nerve paths. Flourens' physiological checks, made without anesthetic or surgical elimination of reflex responses, were hardly adequate to determine this point. In view of these various objections it is obvious that no reliable conclusion regarding central readjustment can be drawn from this single historic experiment of Flourens.

About a half century after Flourens' initial experiment, attempts to repeat nerve cross operations were successful and appeared in the main to confirm Flourens' observations. This apparent experimental success with nerve crossing was soon followed by clinical application, and ever since then numerous scattered reports, both clinical and experimental, have been accumulating in the literature. Although the clinical accounts now far exceed the experimental reports in numbers, it is the latter which in most instances have yielded the more thorough and more widely accepted evidence on the problem of central nervous reorganization.

Results on Hind Limb

Experimental

The sciatic nerve of the hind leg and particularly its two terminal branches, the tibial and common peroneal nerves (internal and external popliteal nerves) have been used frequently in experimental nerve crossing. These two divisions of the sciatic are relatively large nerves, readily accessible, and lie side by side for a considerable distance, making their cross-union easy from a technical standpoint. And, particularly important with respect to the problem of central reorganization, they innervate antagonistic muscle groups. The main dorsiflexor muscles of the ankle joint are supplied by the common peroneal, and the main plantar extensors are supplied by the tibial. Accordingly, a number of studies of partial or complete crossing of these nerves have been undertaken with a view to demonstrating the functional effect of switching the innervation of antagonist muscle groups. At first glance, complete crossing of these nerves might be expected to produce a reversal of foot movement, i.e., dorsi-flexion when plantar extension should normally occur, and vice versa. Instead of such a reversal of foot movement, however, nearly all investigators who have performed complete or partial exchange of the normal nerve connections in this region have until the last few years reported a rapid and complete recovery of normal leg movements.

Complete reciprocal crosses between the common peroneal and tibial nerves were undertaken by Rawa (1885) in cats and rabbits, and by Spitzy (1905) and Osborne and Kilvington (1910b) in dogs. Instead of crossing separately the peroneal and tibial nerves, Kennedy (1899) rotated the distal end of the divided sciatic in the dog 180 degrees and sutured the stumps so that the proximal tibial division was apposed to the distal peroneal division, and vice versa. For comparison, he also reunited the divided sciatic in correct orientation. Separate crosses between tibial and common peroneal in one direction only, i.e., proximal tibial to distal peroneal or the reverse, were made by Rawa (1885) both unilaterally and bilaterally in dogs, cats, rabbits, and pigs.

The proximal stump of either tibial or peroneal nerve was sutured to the distal ends of both peroneal and tibial nerves in the dog by Kilvington (1905) and later by Aird and Naffziger (1939). In these experiments the nerve fibers normally supplying one set of muscles were made to reinnervate not only their original muscles but, by multiple axon branching, their antagonist muscle group as well. Dogliotti (1935) also sutured, in the dog, a small undesignated portion of the proximal stump of the divided sciatic to the entire distal stump. On the basis of apparently successful results in the latter three studies it has been suggested that, in cases of poliomyelitis or of other neurogenic paralyses, a few remaining healthy fibers may be made to reinnervate profitably an extra load of muscles (Billig and van Harreveld, 1943). A somewhat similar effect was secured by Spitzy (1905) in dogs by implanting the end of the distal portion of the divided peroneal into the intact tibial or vice versa, so that severed fibers in one nerve were guided in regeneration to the end-organs of the other nerve with the possibility of additional branches reaching the original muscles also.

Contralateral crosses between the left and right sciatic nerves were performed by Bethe (1905; Bethe and Fischer, 1931) in the dog, with the result that the right leg, at least, became successfully reinnervated by the left sciatic nerve. Contralateral crosses between the sciatic nerves of the dog were also made by Maragliano (1911, 1912). He split the main sciatic trunk in the right leg and crossed one division to the entire sciatic trunk of the left, so that after regeneration the sciatic musculature of both legs was innervated from the right sciatic spinal centers.

Despite the abnormal switching of connections between the central nervous system and the hind limb muscles in the above studies, it was reported in all cases that the animals recovered normal leg movement. Most of the above investigators gave special attention to the problem of the dissociation and reassociation of motor patterns and insisted that normal muscular coordination was perfectly reestablished. Thus it has been asserted that after complete reciprocal crossing of the peroneal and tibial nerves, and after various types of partial crossing and intermixing of the nerve connections of plantar extensor and dorsi-flexor muscles, and even after contralateral nerve crosses between left and right leg, restitution of normal motor function is possible and does occur in the majority of cases. The more outstanding of the above reports have long been widely accepted as conclusive demonstration of the extreme dynamic plasticity and reintegrative capacities of the central nervous system. The recovery of normal function after the switching of these particular nerves is all the more striking since it involves modification of those presumably stable functional associations of the spinal centers underlying the classical hind limb reflexes upon which the familiar laws of reciprocal innervation of antagonistic muscles have been largely based (Sherrington, 1906). It has been taken for granted from these results obtained mainly on the dog that, provided equally successful regeneration of severed nerves could be attained in man, "relearning" might be expected to occur even more readily.

However, certain objections and criticisms to the entire series of above investigations prohibit acceptance at present of any conclusions drawn therefrom regarding central nervous plasticity and reorganization. In none of the above studies was there any detailed analysis of the action of individual muscles before and after operation. The criteria of functional recovery included merely the animal's general use of the limb in walking, running, jumping, and other activities, with at best only a comparison of the use of the operated limb with that of the contralateral unoperated limb. Also there were rarely control experiments to eliminate alternative interpretations. In fact, detailed consideration of exactly what defect the operations would be expected to produce and how much recovery would be anticipated simply from reinnervation without any central readjustment makes it seem very questionable that any central reorganization was involved in the results.

In evaluating this group of experiments, it must, first, be kept in mind that the lower sciatic and peroneal and tibial nerves are distributed to muscles below the knee only, so that it is merely movements of the foot and digits which were affected by the nerve-cross operations. Function of the hip and knee joints was not appreciably impaired. Furthermore, in the animal species used, the dog, cat, rabbit, and pig, movements of the digits in locomotion and other general activity are so negligible that abnormalities of action could easily escape notice. Hence it is primarily to movement of the ankle joint alone that the reports of functional recovery may be said to apply. The ankle joint, by virtue of its structure in these animals, is largely restricted in its range of movement to flexion and extension. There is little need for active dorsi-flexion of the foot in these digitigrade animals in most general activities; the ankle is simply kept in extension and used like a stilt for support. Thus the main requisite for restoring to the dog the use of the hind leg after such operations is a sustained extension of the ankle with sufficient stability to support the body weight.

Such plantar extension with, at the same time, enough resiliency for dorsi-flexion to occur to some extent in the correct flexor phase of coordination is exactly what might be predicted in the absence of central readjustment to follow the complete crossing of the peroneal and tibial nerves, for the following reasons: The peroneal and tibial nerves innervate in addition to the primary flexor and extensor muscles of the foot many other muscles of the shank, including those of inversion and eversion, and those for spreading and flexing the toes, as well as the array of small intrinsic foot muscles. It may be safely presumed that all these additional muscles do not normally work in perfect synchrony with the two primary groups in strict association with one or the other according to their peroneal or tibial innervation. Nor does it necessarily follow, because the primary dorsi-flexor and plantar extensor muscles are larger in mass than the other shank muscles, that the action of their fibers should predominate after crossing. There is evidence that smaller muscles have many more motor fibers per mass unit than do the larger muscles (Clark, 1931), so that the small muscles figure much more prominently in the nerve fiber population than they do as muscles. Moreover, axons which originally supplied very small motor units in small muscles may regenerate into large muscles and come to command motor units of much greater size and strength than those originally supplied. An additional factor contributing to functional confusion is the tendency of individual axons to send multiple branches to different muscles. In view of the foregoing, the crossing of these compound nerve trunks could be predicted schematically to result only in a confused contraction en masse of all reinnervated muscles supplied by both nerves in any leg movement.

Due to the superior strength and mechanical relations of the antigravity plantar extensor muscles, such massive indiscriminate excitation of the shank musculature would lead to plantor extension of the foot, a tense, stiff extension because of the opposed contraction of all muscles about the shank. This extension would probably be further enhanced in time by a permanent contracture of the plantar extensor muscles. The ankle joint seems to be particularly prone to the development of such contractures (Kennedy, 1919; Pollock and Davis, 1933; Sperry, 1941; and others). Massive contraction of the extensors, aided by a contractural shortening of these muscles in adjustment to the natural walking position of full extension, would furnish ankle support possibly even stronger than normal. Though lacking perhaps in adaptable gradations of tension, it would still be somewhat resilient.

Maintenance of plantar extension would be further reinforced in the supporting phase of leg movement in locomotion by extension of the knee. The major plantar extensor muscles inserting on the Achilles' tendon of the heel have their origin on the femur above the knee joint so that extension of the knee simultaneously forces a strong passive extension of the ankle. Conversely, flexion of the knee releases this force and permits the ankle to flex dorsally. Flexion and extension of the knee would thus result in simultaneous passive flexion and extension of the ankle. Since the knee and ankle normally work in unison in these animals, the effect would closely simulate normal function. Such passive movement of the ankle by the knee would show marked improvement after reinnervation had restored tonus and contractility to the paralyzed shank muscles. This gradual recovery of stability of the ankle joint, and even a tendency for passive ankle flexion and active extension to occur in the correct phase of limb movement, would permit a use of the hind limb which to gross observation might well be indistinguishable from normal. Certainly, compared to the complete paralysis immediately following nerve section, or to reversed or spasmodic movements of the joint such as might at first thought be expected to follow nerve crossing, it is understandable that recovery of the use of the limb to this extent might well suggest to many observers that central readjustment had occurred.

Thus the reports on the results of interchanging experimentally the peroneal and tibial nerve connections are open to the general criticism that the use of the leg that appeared to be executed by normal muscle coordination might well have been effected passively by movement of the knee aided by contracture of the plantar extensor muscles, without involving any adaptive readjustment whatever in the central motor coordination patterns. Further points may be cited in support of this interpretation. Schiff (1885) very early objected to Rawa's experiments on the basis that the foot movements were passive, produced by the action of the knee joint. Kennedy (1901, 1914a, 1914b), in later reports following his own earlier work on the sciatic nerve, stated that the reported recoveries in the hind limb leave doubt as to whether they were real or apparent, because after complete section of the sciatic nerve high in the thigh at the level of the trochanter the dog is still able to use the hind leg in walking. He said that the ligaments of the hind leg in the dog are sufficient to support the animals without muscular contraction. He mentioned further that the most noticeable defect after sciatic nerve section in the dog is a tendency for the dog to walk on the dorsum of the paw, but that this is not always present, and if it is, it shows improvement anyway without actual reinnervation of muscles, giving a false impression of recovery. Also Swan (quoted by Sherren, 1906a), after studying the results of experimental section of the sciatic nerve in dogs and rabbits, wrote, "I was at first astonished at how much an animal could move its limb a short time after operation and concluded that misconceptions have arisen from considering the general motion of the limb as indications of the restoration of the nerve."

The unreliability of the above reports of recovery of muscle coordination is further illustrated by the fact that in some cases it was reported (Rawa, 1885; Kennedy, 1897) that good recovery of function occurred within so short a period after operation that the nerves could not possibly have had time to regenerate and reestablish functional connections. Such an obvious error in interpretation is explained by the fact that many of the experiments were carried out before it had become generally recognized that severed nerves, instead of healing together directly, have to regenerate new fibers all the way from the central stump to the periphery (Boeke, 1935).

The applicability of the above criticisms to the experiment of Osborne and Kilvington (1910b), in particular, might be questioned because they studied the hind limb reflexes of their animals after cord transection, mentioned that great care had to be taken to avoid confusion due to mechanical effects of movement of associated joints, and stated specifically that some of the reflex acts they obtained could not possibly be regarded as mechanical and passive. They crossed the peroneal and tibial nerves unilaterally in four young dogs. At first after regeneration there were signs of reversed movements and much incoordination, but slowly the animals learned, in a manner suggesting to the authors "conscious effort and analysis," to effect coordinated movement, until at the end of a year the movements of the operated limb were reported to be as rapid and coordinated as those of the sound limb in walking, running, galloping, and jumping. The spinal cord was transected about a year after the nerves had been crossed, and it was then found that the reflexes of both hind limbs were identical indicating that the corrected coordination of the operated leg had persisted in the spinal state. It was concluded from this that the neural basis of acquired habit may extend to the lower levels of the spinal cord. The experiments were undertaken originally to test whether new acquired coordination patterns can predominate over innate patterns, and it was decided from the results that this is possible if sufficient time (about a year in these cases) is allowed for training.

This experiment is generally regarded as the most convincing of the above series. The observation that coordination was not only recovered but that it persisted after cord transection, as if reorganization had occurred in the lower spinal centers, is extremely significant. The interpretations and conclusions of the authors, however, are hardly acceptable at present without further proof. Of their four animals, one was discarded because the operation was faulty, two others did not survive the spinal transection in good condition, so that apparently only one animal yielded a fully satisfactory record of spinal reflexes. In this case, later anatomical check revealed that some fibers from both nerves had grown back into their own distal stumps, although the action of these fibers was said to be so trifling as to be considered negligible. Despite their statement regarding great care to avoid misinterpretations due to passive mechanical effects from neighboring joints, no specific reason is given why the foot movements they observed might not have been mechanical, nor is mention made of any definite precautionary measures to eliminate such sources of error.

In addition to flexion and extension of the foot, in one case a type of toe-spreading reflex was elicited which was said to be identical in both hind legs. Gutmann (1942) also has demonstrated recovery of toe-spreading in the rabbit after crossing the tibial nerve to the distal stump end of the peroneal. It appeared in the rabbits, however. only when they were held upside down, was very poor at best, and could be elicited only with difficulty. That the recovery of toe-spreading in the upside-down position was due to practice or reeducation is doubtful, and Gutmann furthermore explains that the assumption of central reorganization is unnecessary, since there are motor fibers present in both tibial and peroneal nerves mediating this reflex. One wonders further if muscles innervated by the tibial nerve other than the single muscle involved in toe-spreading are not also active normally in the particular inverted conditions in which the reflex appeared. Fibers of such muscles rerouted into the peroneal group would also produce toe-spreading without need for central adjustment. That a similar explanation is applicable to the results in Osborne and Kilvington's dogs is also possible, but this cannot be said with certainty because the reflex they mention is unfamiliar and was not described in detail.

In any case, the conclusions of Osborne and Kilvington have not been borne out in recent reinvestigations. Watrous and Olmsted (1941) studied the late functional results of crossing the peroneal and tibial nerves in cats and dogs by recording after decerebration the reflex contractions of isolated flexor and extensor muscles. Although the results tended to be somewhat ambiguous and the report has since been cited both for and against reeducation, it would seem a safe deduction that at least the recovered responses were definitely abnormal and incoordinated. Even in control cases in which the nerves had been reunited to their original stumps, the reflex reactions were incoordinated. Obrador (1942a) also crossed reciprocally the peroneal and tibial nerves in cats and dogs. Observation of the animals' stance and gait after regeneration revealed signs of defective posture and incoordination, but the withdrawal reflex and in some cases the support reaction of Magnus were not abnormal to gross inspection. In kymograph recordings of the contraction of individual muscles after decerebration or under anesthesia, contraction of the plantar extensor muscles predominated whether ipsilateral or contralateral afferent nerves were stimulated. The presence of extensive axon reflexes involving muscles of both nerve trunks reveals that Obrador did not achieve his purpose of clearly crossing the two nerves. Even so, he concluded that no visible signs of a marked reorganization and functional readaptation in the spinal levels appear after peripheral nerve crosses. The tests of Watrous and Olmsted and of Obrador after decerebration give no assurance that motor coordination had not been present previous to decerebration. According to what evidence we have at present (Lashley, 1921) regarding the learning process and automatization of habits, decerebration or cord transection would be expected to abolish any reeducational adjustments that might have existed. The results of these more recent tests of decerebrate reactions nevertheless definitely discredit Osborne and Kilvington's previous findings of complete reorganization in the lower spinal levels.

The functional effect of crossing the peroneal and tibial nerves has been examined in the rat by Sperry (1941). Twenty animals were operated on, at ages ranging from 15 days to 80 days. The strength of foot movements upon electrical stimulation of the nerves, as well as the size of the shank muscles 2½ months after operation, indicated that excellent crossed reinnervation was achieved. In none of the twenty cases, however, was there a restoration of normal coordination. All animals exhibited a pronounced stiffness of ankle movement with plantar extension predominating. The picture suggested massive undissociated contraction of all reinnervated muscles. Active dorsi-flexion of the foot, although it could be produced by electrical stimulation of the crossed tibial nerve, never occurred naturally either in reflex or voluntary movement. Gutmann (1942) has since reported a similar result in the rabbit. In the course of time the tense incoordination in the rats, instead of approaching normal reciprocal movement, gradually became worse. Especially in the younger, more rapidly growing rats the persistent extension of the ankle resulted ultimately in an anatomical shortening of the plantar extensor muscles until the rats walked about on their digits with the ankle fully extended. These results are particularly interesting because the nature of the recovery, obviously maladaptive in the rat, would be quite beneficial and would closely simulate the normal limb action of a digitigrade animal like the dog, on which most of the older experiments were carried out. No sign of reeducative correction of the function of the crossed peroneal and tibial nerves was evident in the rat.

It has been shown further that with more carefully designed operative measures, the crossing of nerves to the flexor and extensor muscles of the shank in the rat results in a clear-cut reversal of ankle movement (Sperry, 1941). In 10 animals, 8 operated on unilaterally and 2 bilaterally, individual muscular nerve branches to flexor and extensor muscles were dissected free and crossed to specific antagonist muscles, the anterior tibial muscle and the gastrocnemius muscle. In addition, all remaining muscles acting on the ankle were excised to prevent their action from masking that of the test muscles. This crossing of individual muscular nerve branches, instead of the whole peroneal and tibial trunks with their heterogeneous combinations of fibers of varying function, accompanied by excision of all non-test muscles acting on the joint, tended to produce a more precise result and at the same time eliminated several major sources of trick movement.

Under these more critical conditions the functional effect after nerve regeneration was a clear-cut, positive reversal of foot movement in all activities, voluntary as well as reflex. Dorsi-flexion occurred when extension would have been serviceable, and plantar extension when flexion should normally have occurred. This diagrammatic reversal of foot movement never reverted to normal. It persisted without any signs of correction despite training conditions and surgical measures designed to force out reeducational adjustment. The majority of cases were kept until the approach of senescence. They failed not only to make a positive correction of the maladaptive responses, but even to inhibit the reversed reactions, which were decidedly more detrimental than would have been no movement at all.

Failure to correct such obviously maladaptive reversed movements is to be distinguished from failure to correct less serious motor incoordinations in situations in which, as after crossing the peroneal and tibial nerves in animals like the dog and cat, abnormality of movement is hardly manifest and detracts only slightly from the animal's use of the affected limb. The incentive for education afforded by markedly reversed movements is much stronger, and hence lack of readjustment under these conditions is more striking proof of the lack of readaptation capacity. It must also be emphasized that the anatomical disarrangements and the central reorganizations required to correct them are much less extensive in character after nerve crosses involving individual muscular branches, than after the unselective crossing of large heterogeneous nerve trunks. The central readjustment required after crossing individual muscular branches may be compared with that required after muscle transposition (see below), in contrast to the complete dissociation and reintegration from the neuron level up needed after haphazard regeneration and crossing of compound nerves. Finally, the rats' failure to improve their condition by simply inhibiting all foot movements is to be distinguished from the failure to achieve the more complex task of effecting positive reestablishment of correct movements. That the rats did not learn even to suppress the reversed responses either in simple deliberate movements or in reflex reactions under the above conditions is particularly convincing evidence of the limitations of central adaptation capacity.

Besides the peroneal and tibial nerves of the hind limb, the obturator and femoral nerves have also been subjected to partial and complete crossing. These nerves innervate antagonistic muscles of the thigh, the obturator nerve supplying muscles for adduction and flexion and the femoral nerve muscles for abduction and extension. Spitzy (1905) produced partial crosses between these nerves in the dog by implanting the distal end of the divided crural nerve into the obturator. He reported good recovery of locomotion. A more thorough study of the effect of crossing these nerves has been made more recently by Anokhin and Iwanow (1936b; Anokhin, 1935a). They made complete reciprocal crosses in the dog, both bilaterally and unilaterally. During the first two months after operation the dogs were unable to support themselves on the operated legs. Beginning about the third month, the use of the hind limbs gradually improved, until at the end of a year locomotion was indistinguishable from that of normal animals. Even in the absence of the corresponding area of the motor cortex a positive recovery was finally achieved, although the reintegration was said to proceed more slowly. The authors concluded that the flexor and extensor motor horn cells had changed function as a result of local reintegration processes within the spinal cord, and that later, following the order of ontogenetic development, these new spinal patterns were brought into relation with cortical processes.

That any central reintegration either in the spinal cord or at higher levels had actually occurred in the animals of Anokhin and Iwanow may justly be questioned on the following grounds: According to the authors' diagrams of the anatomical conditions before and after operation and after regeneration, the nerve crosses were not distinct. A sizable bundle of fibers of the sciatic nerve was crossed along with the obturator nerve into the femoral muscles. Also the precautions taken to prevent regeneration of fibers back into their own distal stumps were not successful. Moreover, the nerves crossed do not innervate the entire thigh musculature acting upon the knee joint. Strong flexion of the knee would still be possible, for the nerve supply of the main flexor muscles remained intact. This would explain the good flexion reflex to electric shock which was reported to be present after recovery. The most serious detectable effect of the operation would be inability to use the knee for support, due to paralysis of the quadriceps extensors. The recovery of tonus and possibly the establishment of a persistent contracture in these muscles after reinnervation by the obturator nerve, apart from any central reorganization, would aid greatly in restoring strength and steadiness to the joint, and thereby its use in locomotion. It has not been shown and cannot be assumed that the muscle groups supplied by the obturator and femoral nerves contract in perfect antagonism in the locomotion of the dog. Considerable co-contraction may be present in the muscle groups of these two nerves, with the result that the knee extensors after reinnervation would naturally be activated to some extent in the appropriate phase of limb movement. This possibility of the quadriceps having been reinnervated by motor fibers whose normal central timing was not inappropriate for these muscles was further favored by the inclusion with the obturator nerve of fibers belonging to the sciatic trunk. Furthermore, the action of sound muscles acting on the thigh and lower leg when these are fixed at one end by the ground and at the other by the trunk could exert considerable extensor force at the knee joint. Watrous and Olmsted (1941) have suggested that possibly normal use of the limb in these experiments was brought about by muscular compensation In this connection, J. E. Stewart (1925), after transplanting the nerve supply of thigh muscles in the dog, found that dogs in which the sartorius muscle had been cut and the rectus femoris paralyzed, got about perfectly normally after a few weeks, showing no limp whatever in walking. He went on to warn that, as a consequence, experiments the results of which are determined by the ability of the animal to use the extremity would seem to be unreliable. Anokhin and Iwanow did not check these alternative possibilities of interpreting the recovery they observed.

It is thus quite conceivable that recovery of the use of the limb in locomotion in these cases may have been due to the compensatory function of sound muscles plus massive undifferentiated contraction or contracture of the affected muscles, imparting a generalized background stability to the affected joint. With such stability, absence of normal muscle coordination would be difficult to detect in locomotion and general activity where the lower leg needs to serve only for support. Incoordination, if present, however, might show up in specialized movements, and in this regard it is truly "interesting," as the authors state in describing a typical case, "that two years after the establishment of new relations in the spinal cord, the animal moves and runs like any normal animal but is nevertheless incapable of performing the finer movements which require the work of specific muscle groups." They conclude that movements of the extremity in the total locomotor act are therefore different from isolated movements performed when the animal is at rest. This is very probably true, but it is doubtful whether the rapid automatic complicated coordination involved in locomotion would have been recovered by learning, while the easier task of performing, while at rest, simple isolated movements with a comparatively few muscles remained impossible. Such a conclusion would be directly contradictory to conditions in man (Scherb, 1928a, b). It seems just as likely that the incoordination merely became more obvious in specialized movements, and that it was also present but not detected in other movements. Spitzy's less detailed account of recovery after partial crossing of the obturator and femoral nerves in the dog is even less convincing.

Trick movements and other sources of error in estimating recovery of muscle coordination. It is clear that past reports of good recovery of normal muscle coordination following experimental interchange of hind limb nerves have been generally invalidated by the erroneous assumption that ability to use a limb in seemingly normal fashion implies the presence of normal muscular coordination and coincidentally by the failure to present convincing evidence that the recoveries actually involved an adaptive shift in the function of the crossed nerves. As already mentioned, there are a number of deceptive factors other than recovery of normal muscle coordination which may tend to restore the utility of a limb and hence must constantly be watched for in estimating the quality of motor recovery.

The majority of the items tending to cause errors of judgment as to recovery of motor function have been included under the heading of "trick movements," otherwise referred to as "compensatory," "supplementary," "vicarious," "substitutionary," "accessory," or "anomalous" muscle function. Trick movements have long been recognized (Pitres, 1916; Hughes, 1918; Woods, 1919; Pollock, 1919, 1922; Jones, 1919; Coleman, 1920; Ingham, 1920; Forrester-Brown, 1920b; and others) as a frequent misleading symptom of the utmost importance in the diagnosis and treatment of peripheral nerve wounds.

The methods most commonly cited by which trick movements can be produced are the following: (1) Muscles supposed to be supplied only by a nerve which has been completely divided may continue to function in whole or in part by virtue of anomalous nerve supply. Practical experience with peripheral nerve injuries has taught that the classical standardized descriptions of muscular innervations are not to be relied upon in diagnosis of nerve injury and recovery (see Highet, 1943). (2) Remaining sound muscles, or combinations of these, whose action resembles that of the affected muscles can often, with or without practice, be made to reproduce the actions previously performed by the affected muscles. (3) The resiliency of tissues holding a joint often permits movements to be made in the direction of the action of the affected muscles merely by relaxation of sound antagonist muscles. The release of active contraction of the antagonists is followed by a passive rebound of the limb segment to or beyond the resting position. (4) Owing to the mechanical relations of tendons and ligaments of the limbs, displacement of one joint may frequently cause a passive movement of another joint farther distal or proximal. This passive mechanical effect is due primarily to the presence of muscles or tendons stretching across more than one joint. (5) Movements, particularly of the heavier limb segments, may be produced by gravity. Extension, for example, may be obtained simply by allowing a limb segment to fall from the flexed position, or vice versa, depending on initial posture. (6) Movements, of the distal joints particularly, may be produced by momentum. The distal segments may be flung by more proximal segments in flail-like fashion into a desired position. (7) Movements may be produced by pushing against or pulling on, or otherwise using an outside object such as chair, desk, floor, or examining table as a fulcrum or other mechanical aid to effect a movement no longer possible with the affected muscles alone. (8) At joints used primarily for stability and support or where rigidity is more beneficial than a loose paralysis, recovery may be affected by processes of fibrosis, contracture, or even ankylosis of the joint. Compared with the initial flaccid paralysis, the resultant steadiness may bring about a great improvement in the general utility of the limb. (9) The action of healthy antagonists may be suppressed to restore a more favorable balance of power and so effect improvement that might erroneously be attributed to recovery in the paralyzed muscles.

By any or all of the above means, separately or in combination, a patient may, with continued practice and in the complete absence of any functional recovery of the divided nerves, come to perform with considerable smoothness and little apparent difficulty or hesitancy movements which in the period immediately following nerve division seemed impossible. Most of these factors contributing to trick movements can, by appropriate measures, be eliminated in clinical examinations, and in increasing degree this is being done routinely in the pre-operative diagnosis of nerve lesions. It has not been the practice, however, to take similar precautions in anywhere near equal measure in judging the degree of functional recovery after nerve suture and regeneration. On the contrary, only the most general description of functional improvement has usually been given. One reads, for example, that the patient was able after recovery to play his banjo, ride a bicycle, or return to his job, or the operated dogs could run and jump, could hardly be held back with a leash, or could be exercised on the street without attracting attention. Marble, Hamlin, and Watkins (1942), among others, justifiably deplore the general lack and inconsistency of criteria of recovery which have existed in the past, indicating that it has been the greatest stumbling block in the study of nerve repair, whereupon they offer as a new standard for estimating recovery another vague and unanalytical criterion, namely, "a hand which would prove useful for ordinary occupation and average everyday life." Establishment of a truly fundamental and useful body of knowledge from which generalizations and predictions can be made regarding the possibilities and limitations of motor recovery after nerve regeneration must be founded upon much more specific and basic criteria of recovery, expressed in terms of the contraction patterns of the affected muscles themselves.

It remains to be pointed out that the foregoing list applies to cases in which no reinnervation of the paralyzed parts has occurred. The problem becomes more complicated, and additional misleading factors must be taken into account, in analyzing coordination after reinnervation has been established. A number of the above possibilities for producing trick movements are considerably enhanced by the return to the paralyzed muscles of contractile strength, tonus, or the active contracture which often follows reinnervation. When the recovered movements can be definitely ascribed to the reinnervated muscles there is still the question of whether the timing of the motor impulses involved has actually undergone any adaptive modification. Correct movements may be due to the firing of nerve fibers whose original muscles contracted synchronously with the new muscles. The synergism and antagonism of muscles is a complicated matter; many so-called antagonists actually show co-contraction in a large proportion of movements. The lack of thorough knowledge of muscle kinesiology in man except for the simplest of movements, is a drawback in interpreting the results of nerve crossing, particularly in the limb.

Clinical

By the old method of lateral implantation the tibial nerve has been made in man to supply both its own musculature plus that of the divided peroneal. And contrariwise the peroneal nerve has been made to supply its own muscles plus the antagonistic muscles of the tibial nerve (Spitzy, 1907). Also the sciatic nerve, after severe partial degeneration, has been cut or crushed in order that the remaining healthy fibers might reinnervate through multiple branching an additional supply of new end-organs (Dogliotti, 1935; and others). Implantations resulting in partial crossing have also been made between obturator and femoral nerves in man (Spitzy, 1905, 1907), and Maragliano (1911) crossed a branch of the crural nerve of the left leg contralaterally to the distal end of the entire crural nerve of the right leg. The reports of recovery in these and similar cases, as well as in those more numerous cases in which severed nerves of the leg have been reunited to their own stumps, imply that some improvement in function was obtained in a majority of cases from the operations. On the whole, however, recovery in man has definitely been disappointing compared to the complete success frequently reported in animal experiments. This is usually attributed to the fact that optimum conditions for nerve regeneration prevail in experimental nerve suture, whereas quite the opposite is apt to be true in the repair of accidental nerve lesions. Failures, when mentioned, have usually been attributed to factors preventing complete nerve regeneration.

Those accounts, on the other hand, in which good recovery of function was said to have been achieved have not been adequate for use as evidence of central reorganization after nerve regeneration, for the following reasons: (a) Recovery has been judged frequently merely by the increase in size of the reinnervated muscles, by the muscular contractions elicitable by electric stimulation, or by the patient's ability, on command, to bring into contraction the reinnervated muscles along with others of the region, with no regard whatever for the differential coordination of the reinnervated muscles in natural movements. In cases where natural activities have been considered the use of the affected parts is described vaguely as "improved," "able to walk without clumsy appliances," and in other such non-specific terms. (b) The normal contraction phase of various muscles in the highly differentiated movements of man is difficult to ascertain without special methods and has not been worked out except for the simplest of movements. It is thus difficult to know in many cases whether recovery of adaptive function of an abnormally innervated muscle in the performances described implies readjustment in the function of the dislocated nerve or not. (c) Although most of the clinical reports have devoted much space to methods of exposing, handling, and reuniting the nerves, the description of surgical procedure generally does not include those details most important for evaluating the functional results, such as the exact level of suture with respect to the inclusion or omission of various nerve branches, the muscles affected and those not affected, and similar details. (d) Reciprocal crosses are, of course, not undertaken, and if nerve crossing is used at all, attempts are made so far as possible to use nerves synergic in function which subsequently require no reeducation. (e) Control cases and anatomical checks after observation have been lacking. (f) Practical difficulties in following up the later results of operations have seriously detracted from the completeness of reports of recovery in man. (g) Instead of being careful to prevent regeneration of the original nerve connections as in experimental preparations, any measures possible have naturally been taken to promote such regeneration. (h) In the great majority of reports of recovery after regeneration of limb nerves, the nerves have been reunited to their own stumps, which permits branching of single axons to several of any of the affected muscles. It cannot be determined under such conditions whether a failure to achieve dissociated muscle action has been due to axon branching or to central nervous implasticity. Nor can it be known to what extent any successful recovery may have been due not to reeducation but to chance termination of fibers on appropriate end-organs. (i) Surgeons have naturally been more inclined to report their apparent successes than their failures. Sargent (1920) mentions that a man examining his own cases could not help being prejudiced in favor of seeing good results. Any such bias becomes especially important when there are no standardized objective criteria to limit and control description of the results. (j) Where the question has arisen as to whether reeducation under given postoperative conditions would be possible, it has generally been presumed that the answer is affirmative, and as evidence have been cited most often, not clinical results, but the old animal experiments of Flourens, Rawa, Kennedy, Osborne and Kilvington, and others. (k) That the occurrence of central readjustment cannot safely be inferred from the uncritical clinical accounts of "good recovery" is further emphasized by the fact that, even more often than in experimental studies, excellent recovery has been reported within periods from a few hours to a month after operation (Foerster, 1918; Perthes, 1922), well before the divided nerves could possibly have regenerated and restored function to the paralyzed muscles. Such obvious mistakes were no longer made, of course, after it had become more generally appreciated that it takes considerably longer for divided nerves to reestablish functional relations. Although errors of this kind have since been restricted to reasonable time limits they have not been eliminated. Coleman (1941), for example, mentions that he has frequently been impressed in delayed exploratory operations by finding nerves still completely divided when repeated clinical examinations had appeared to justify the assumption that these nerves were recovering their function spontaneously.

Results on Forelimb

Particularly in man, but also in the lower vertebrates, possibilities for reeducation would appear to be more favorable in the case of the forelimb than in the hind limb. The greater variety and differentiation of forelimb movements, the greater influence of the cortico-spinal system on forelimb movement, the larger cortical representation of the forelimb, the increased degree to which forelimb movement is subject to visual control, the less automatic or more voluntary nature of forelimb movement, and, in the quadrupeds especially, the more direct effect of forelimb movement on vestibular and visual orientation and equilibrium would all presumably favor the forelimb in the detection and correction of errors in motor coordination. Scherb (1938), in discussing central nervous reorganization after muscle transplantation in man, emphasizes that there is a decided difference between the upper and lower limbs and that reeducation is much easier and becomes more complete after transplantation of arm muscles than of leg muscles.

Experimental

The great majority of previous workers who have studied the effect of crossing forelimb nerves experimentally have not reported any permanent discoordination. On the contrary, in the forelimb as in the older hind limb studies, it has been maintained with few exceptions that a good recovery of normal coordination follows nerve crossing. Most of the experimental work has been carried out on the dog, and the nerves usually selected for crossing have been the large trunks of the radial, median, and ulnar nerves, and occasionally the musculocutaneous nerve. These nerves supply all muscles below the elbow. They also give off branches high in the brachium to the muscles of the upper arm, but in most of the experiments the nerves have been cut and crossed in the middle of the brachium or near the elbow, leaving intact all branches to the upper arm muscles. The operations have been designed to test the effect of interchanging in various ways the innervation of the extensor muscles of the forearm, supplied by the radial nerve, and the antagonist flexors, supplied by the median and ulnar nerves.

Reciprocal crosses between the median and radial nerves in the dog were carried out by Stefani (1886). He reported a recovery of voluntary, coordinated movements, ability to hold a bone or give the paw, although the nerves for flexion had come to serve for extension and vice versa. Gunn (1886) crossed the central end of the divided median nerve to the distal ends of both radial and ulnar nerves in the dog. Subsequently a perfect condition of motility was observed. Time and practice, according to him, may bring order out of the confusion created by abnormal innervation.

Cunningham (1898) made reciprocal crosses in the dog between the radial nerve supplying extensor muscles and the median and ulnar nerves supplying flexors. He found incoordinations amounting in some activities almost to a reversal of normal movement. These incoordinations persisted for 15 months without any correction. On the basis of his results he flatly contradicted the previous conclusions that correct function is recovered after nerve crossing. Later Kennedy (1901) repeated nerve crosses in the dog similar to those of Cunningham, except that he included with the median and ulnar the musculocutaneous nerve in order to be certain that there would be no muscles remaining below the elbow with innervation intact. Contrary to Cunningham, he found a complete return of coordinated movements. Coordination of the operated limb after recovery was said to be perfect in walking, running, jumping, and in running rapidly up and down stairs. The paw was also used correctly in isolated movements of the forelimb.

Satisfied that it had been demonstrated that nerves crossed to antagonist muscles could give up their old function and take on a new function suited to the antagonist muscles, Kennedy (1914a, b) undertook experiments to find out if nerves were capable of mediating both their old function and at the same time a new function also, i.e., if a nerve could serve correctly both its original muscle group plus the antagonist group. He considered inconclusive the older experiments of Kilvington (1905) on this question, cited above. He cut all four nerves of the forelimb and connected the distal ends either to the central stump of the radial nerve or to the central stumps of the median, ulnar, and musculocutaneous nerves in order that all muscles below the elbow would be supplied in some animals from extensor centers only and in other cases from flexor centers only. He again reported good recovery of coordination and concluded that in the limb of the dog, when the nerve supply of one group of muscles has been eliminated, the nerve of its antagonistic group may be used to supply both groups and that under these conditions coordinated movements may be restored. Thus, with only one exception, it has been concluded from the above group of experiments that nerve regeneration to foreign muscles in the forelimb of the dog is followed by a recovery of normal coordination.

The accounts of good recovery are subject to criticisms similar to those raised against the reports of complete recovery in the hind limb. Only a small number of animals was employed in each study. The results were highly variable, with often as many failures as successes. The failures were attributed to contractures, faulty regeneration, stretching of ligaments, etc., and were discounted. As an index of recovered muscle coordination, the investigators in all cases relied upon the animal's ability to use the operated limb in various uncritical activities. The muscles of the proximal joints of the limb, where most movement occurs in locomotion and general activities, retained their normal innervation. Recovery of good use of the limb in these cases was dependent, not upon restoration of any refined differential or reciprocal movements, but merely upon the maintenance of a steady supporting position of one distal joint, the carpal joint. With the paw placed palmar surface down on the ground, the body weight tends to extend, i.e., dorsi-flex, the carpal joint passively. Over-extension of the joint, however, is prevented by the mechanical arrangement of bones and ligaments, so that much support is obtained in the extended position without any muscular activity at all. The extent to which muscular action can be dispensed with and not seriously affect use of this joint is illustrated by the following: Howell and Huber (1892), after crossing the median and ulnar nerves in the dog, noted that on the second day after the operation, with both median and ulnar nerves cut and crossed on the left side high in the arm and also with the ulnar cut on the right side at the elbow, there was little evidence of paralysis or even awkwardness. Before the end of the first week the closest scrutiny could detect no abnormality of movement, except possibly in running upstairs, and it was not certain whether this was due to over-zealousness or to the unusual innervation. Cunningham (1898) also crossed the ulnar and median nerves in the dog in preliminary experiments, and found that 4 days after the operation one could hardly see any difference in the forelimb movements. Gunn (1886) excised a section of the ulnar trunk and could find no impairment of motion in the parts supplied by the ulnar; and in his nerve cross experiments he reported that even the parts supplied by the median nerve, whose distal stump had been excluded from the cross-sutures, recovered from their paralysis. Thus according to observations of the type on which the conclusions regarding recovery were based, both the large median and ulnar nerves and their muscles comprising the greater mass of the forearm musculature can be completely dispensed with and cause no noticeable defect in the dog's forelimb coordinations. Some function of the radial nerve is of aid in maintaining sufficient extension so that the paw lands on the ground palm down, but according to Osborne and Kilvington (1910a) good recovery may be effected in the complete absence of this extensor nerve also, even when the lack of muscle balance remains unremedied with the antagonist flexors intact.

It is probable that the natural mechanical stability of the carpal joint demonstrated by the foregoing would be further enhanced by the trophic changes in the muscles and connecting and supporting tissues, particularly with the use of corrective plaster casts, as in Kennedy's experiments. One would hardly anticipate a pure reversal of movement as a result of crossing these large compound nerves supplying the entire array of antibrachial and intrinsic paw muscles. The return of tonus and mass contraction to the reinnervated muscles would additionally increase the joint's stability, provided an overbalanced flexor contraction was prevented in the early stages of recovery. The role of complementary muscle action in the more proximal joints and in more widespread regions of the intact system, in covering up and minimizing any slight defects that were present, would also aid the appearance of recovery.

Stefani reported signs of recovery as early as the 30th day after crossing the median and radial nerves; Gunn found paralysis disappearing in less than 4 weeks; and Kennedy obtained a complete return of coordinated movements, as exhibited in walking and running, as early as the 32nd day after cutting and crossing all four major trunks of the forelimb at the level of the elbow. That the nerves had regenerated and the reinnervated muscles begun to function effectively at such early dates appears extremely doubtful (cf. Gutmann, 1942).

All the foregoing discussion, indicating the unreliability of the conclusions that central readjustment has followed the crossing of forelimb nerves in the dog, is supported further by the opposing conclusion of Cunningham, who used a larger number of animals and who appears to have attempted a more careful analysis of both the anatomical and functional results of his operations.

Contralateral crosses between nerves of the left and right forelimb affecting muscles acting on the elbow as well as on the carpal joint were made by Osborne and Kilvington (1910a). In one dog they sutured the proximal stump of the left radial nerve cut as far peripherally as possible to the distal stump of the right radial nerve cut as far centrally as possible. In a second dog they attempted to suture one of the brachial cords to the whole right plexus, but subsequent dissection revealed that only an anterior portion of the right plexus had been included. On examination ten months after operation, coordination, as demonstrated by ability to walk and run naturally and to use either forepaw to hold down a bone, was found to be very good in both animals. It is perhaps more surprising that in this experiment recovery was obtained on the left side, where the nerve was removed without substitution, than that it occurred on the right side with crossed innervation. Apparent recovery on the left side at the same time renders meaningless their inferences about recovery of coordination in the right limb and discredits their conclusion that the experiments demonstrate that an interchange of function can readily occur in the motor centers of the cerebral cortex. The utter unreliability of most of these early uncritical accounts of recovery after nerve crossing is obvious.

Perhaps the most striking recovery observed to follow the crossing of limb nerves is that reported more recently by Barron (1931–1934) after anastomoses between the fore and hind limb nerves of the rat. Accepting the earlier reports of complete recovery of normal motor coordination after interchange of spinal nerves, Barron made nerve crosses for the purpose of studying particularly the role played in the "relearning" process by the sensory fibers of the redistributed nerves. He crossed the median and ulnar nerves of the forelimb into the hind limb, uniting them to the distal end of the divided sciatic nerve in some cases and in others to the distal end of the divided femoral. He also made crosses from the hind limb into the forelimb by uniting the central end of the posterior tibial nerve to the peripheral end of the median and ulnar nerves. Results were similar in the different types of cases.

Nerve regeneration was at least partially successful, and recovery of muscle function in the region of the redistributed nerves was reported in 18 of 37 cases. Contractions of the abnormally innervated muscles were at first always associated with movements of the limb in which the nerves were originally distributed. These associated movements in time became partially dissociated in 10 of the 18 cases, and in 4 of these 10 animals the dissociation of movement became complete. In these 4 cases, after relearning had occurred, it was impossible to get any associated movements whatever even by violent stimulation. The movements of the limbs were reported to be completely coordinated within themselves and also normal for their position. Suspecting the number of sensory fibers in a regenerated nerve to be an important factor in this relearning, Barron effected partial deafferentation of the limb from which the redistributed nerves originated. This was done in 6 additional animals prepared especially for the purpose, and in all cases there followed, as anticipated, a decrease in the degree of dissociation previously achieved by learning, which in 3 of the 6 extra cases had gone to completion. From these results it was concluded that associated movements after nerve crossing can be avoided by using nerves which have a large proportion of sensory fibers.

In order to connect fore and hind limb nerves, the central stump must be cut far distally and the peripheral stump far proximally. Therefore fibers from a few small muscles of the distal segment of the original limb are forced to supply many muscles both large and small distributed over several segments of the foreign limb. That recovery of normal coordination by learning could occur under these conditions would indeed be remarkable. It is particularly significant, from both the practical and theoretical viewpoints, that the relearned coordinations should persist without relapses even in sudden reflex reactions to violent painful stimulation. Learning of new motor habits can hardly reach a more complete stage.

Unfortunately, lack of detail in describing the responses precludes consideration of alternative interpretations and obliges one to take as they are given the general statements of complete recovery. It can only be pointed out that the observations and conclusions remain unreconciled at present with other more rigidly controlled results obtained after nerve crossing and muscle transposition in the rat (see below), in which it was found that under conditions decidedly more amenable and conducive to reeducation than those prevailing in the foregoing experiments the rat failed completely to restore any semblance of normal coordination. It would appear, according to Thorburn (1920a), Buzzard (1921), Ford and Woodhall (1938), Bristow (1941) and others, that even man lacks the extreme reeducative capacities ascribed to the rat in the above report.

To obtain a simple situation easy to correct by learning, Sperry (1942a) crossed in the rat the nerve of the biceps flexor muscle of the upper arm to the nerve of the antagonistic long triceps extensor muscle. All other brachial muscles acting on the elbow were excised, leaving in the upper arm only the triceps muscle innervated by the biceps nerve. In addition, the contralateral forelimb, ipsilateral hind foot, and the tail were amputated in order to make the animals more dependent on the operated limb. Control animals were similarly prepared, with the triceps muscle retaining its own innervation. In order to support themselves on the test limb with the dexterity of the control cases, the experimental animals (seven cases) had merely to learn to excite the biceps motor neurons when normally they would activate the triceps neurons. The nerves of only one muscle were involved; no reciprocal adjustment was required; and this type of nerve operation, like muscle transposition, did not necessitate the extreme dissociation and reintegration of functional properties at the cellular level which must follow the random regeneration of heterogeneous nerve trunks. Nevertheless, the crossed nerves continued to discharge in their original flexor phase of limb movement, regardless of the fact that this now produced elbow extension instead of flexion. The animals never learned to use the reinnervated triceps muscle in the extensor phase to support themselves on the operated limb like the controls. Action potential analysis thirteen months after operation showed clearly that the extensor muscle was still contracting without correction in the flexor phase of locomotion and of other movements. Operations in which nerve crossing was combined with muscle transplantation to produce a reversal of elbow movement in both directions, requiring a more complicated type of adjustment, were also followed by permanent discoordination without any corrective adjustment in the contraction of the reinnervated muscles (ten cases).

Clinical

Improvement in function has been reported in man after partial nerve crossing produced by the method of implantation or by direct neurotization of paralyzed muscles at various levels of the arm from the brachial plexus to the distal nerve branches of the finger muscles (see Sherren, 1906b; von Hacker, 1914; von Hofmeister, 1915; Köllicker, 1917; and others). In some cases at least (Sick and Saenger, 1897; Spitzy, 1907, 1908; Hayward, 1917), the authors were convinced that the observed improvement involved readjustment in the central associations of the crossed nerves. These early clinical accounts are uncritical and in general open to censure on the same grounds as those of recovery in the leg. There is therefore little use in speculation regarding the authenticity of the central readjustments inferred. The more recent reports of functional recovery after nerve regeneration in the limbs of human patients are more analytical in some cases. On the whole, they tend to contradict the optimistic conclusions of the early workers. They deal with recovery, however, not after nerve crossing or lateral implantation, but after straight reunion of the ends of the same nerve, and hence their discussion is referred below to the separate treatment of that subject.

Results in the Region of the Facial Nerve

The reports on the results of nerve crossing and nerve grafting for correction of facial paralysis provide by far the most reliable and most numerous data on motor recovery after nerve regeneration in man. The clinical accounts of the quality of functional recovery in the face may be accepted with much greater confidence than reports of recovery in the limbs. Some of the reasons for the superiority of the records of recovery in the region of the facial nerve may be listed as follows: (a) Defects in the quality of the recovered function show up more strikingly in the face than in the limbs and are usually of greater concern to both patient and surgeon. This has focused more attention on the *quality* of functional recovery in the face. (b) Facial movement is a much more delicate indicator of underlying muscle coordination than is limb movement, because the facial muscles are inserted to the skin and other lightweight, easily movable structures. In the face the slightest contractions and twitches register an observable effect. (c) The inaccessibility of the central end of the facial nerve in the temporal bone, and other factors, have fostered the practice of crossing foreign nerves to supply the paralyzed muscles to a much greater extent in the face than in the limbs. The advantages of nerve crosses over straight reunion of a single nerve, for determining the possibilities of central readaptation after foreign innervation, have been mentioned. (d) The right-left symmetry of facial movements and the close proximity of the control reactions on the normal side of the face make comparison between operated and normal sides easier, more accurate, and also more valid than comparisons of recovered limb movements with contralateral or other controls. For the same reason, the establishment of criteria of recovery presents no such problem in the face as it does in the limbs. (e) The greater frequency of facial nerve paralysis and the earlier application of nerve crossing methods for treatment have furnished a longer and more extensive clinical background of experience. (f) Not only is there more material on which to base conclusions, but this material, due to standard procedures of operation, is much more uniform and comparable than is that on recovery in the limbs. (g) Normal recovery cannot be approximated by mass contractions, contractures, fibrosis, etc. Recovery at all approaching normal function demands differentiated contraction of the affected muscles in distinct patterns. (h) Errors of interpretation due to anomalous innervation, not uncommon in the limbs, are largely eliminated in the face. (i) The possibility of executing trick movements with the aid of gravity or inertia is obviously greatly reduced. (j) In the face, there is much less chance for remaining healthy muscles to simulate the action of the affected muscles. (k) Finally, but by no means least important, is the fact that any observer will have become accustomed through life-long experience to reading the subtlest variations of facial expression and may therefore without special training be relied upon to detect even the slightest distortion or defect of coordination, which is not at all true in the case of limb movement.

For the above reasons the present status of our knowledge of motor recovery after nerve regeneration in man is based largely upon the results of reinnervation of the facial muscles. The experimental observations are closely associated and in the main consistent with the clinical records, so that the two may be considered together. The large numbers of recorded cases prohibit separate consideration of individual results but permit a more summarized discussion.

The nerves first tried and ever since most commonly employed as substitutes for the paralyzed facial nerve have been the spinal accessory and hypoglossal. Early in the history of these nerve cross operations, it was noticed that after reinnervation by the spinal accessory nerve of the shoulder the facial muscles tended to contract in association with shoulder movements rather than with the normal facial expressions of the opposite side. Similarly, when the hypoglossal nerve of the tongue was used, contraction of the facial muscles became associated with tongue and chewing movements. Thus it soon became obvious that the transplanted nerves retained the central timing which was suited to their normal end-organs, instead of automatically taking on new functions adapted to their new end-organs. Among the early reports (Sherren, 1906b; Kennedy, 1911a), it was claimed in a small minority of cases that no such associated movements developed, but these claims have not been confirmed. By now it has become generally agreed that associated movements must be accepted as an inevitable result, occurring invariably in all successful cases, after crossing the hypoglossal, spinal accessory, glossopharyngeal, or other somatic motor nerves to the facial nerve (Ballance, 1923–1932; Ballance and Duel, 1932; Duel, 1932, 1933; Ford and Woodhall, 1938; Coleman, 1940).

There remains the question of whether or not these abnormal associated movements can eventually be corrected by reeducation. Some of the early reports were optimistic with regard to this point. Kennedy (1911a, b), for example, claimed restoration of voluntary dissociated face movements in dogs, monkeys, and in human patients after crossing the hypoglossal or spinal accessory nerves to the facial nerve. He reported recovery not only of voluntary closure of the eyelids but also of reflex blinking in a human patient, and also in animals in which the reflex persisted under light anesthesia. Frazier (1924) has pointed out that the recovery of these subconscious reflex reactions in Kennedy's cases is indicative of much more complete and stable central reorganization than is recovery merely of voluntary movements.

It is significant that these early reports of recovery of normal facial movement were based largely on the restoration of eyelid movements. Closure of the eylids closely simulating normal reactions may frequently be observed in persons with complete facial paralysis. These "trick" movements of the eyelids may be produced by relaxation of the levator muscles of the upper lid aided by retraction of the eyball (Cushing, 1903; Kennedy, 1911a) or, according to Bender (1936), by active contraction of the orbicularis muscle itself through an extra nerve supply via the levator branch of the oculomotor nerve. Whatever their mechanism, the presence of these movements in complete facial paralysis destroys confidence in those assumptions that the recovery of lid closure responses involved any readaptation in the function of the crossed nerves. Recovery of complete tonus or slight contracture in the orbicularis muscle, after nerve regeneration, as well as improvement in the "trick" mechanism through increase in strength of the muscles concerned and through greater control over their contraction, could lead to gradual improvement in function over a period of time which might easily be mistaken for reeducation involving the function of the crossed nerve itself.

It is generally agreed now that the early reports were inclined to overemphasize the few meager signs of good recovery that could be found and to omit mention of the obvious shortcomings of the results. Although optimism regarding the possibility of restoring normal facial movements with practice has been expressed more recently in isolated instances (e.g., Foerster, 1930; Phillips, 1938; Goldstein, 1939), the prevailing opinions at present are less hopeful. The most extensive investigations of the late results of facial nerve substitution have been carried out by Ballance. One of the first to attempt a clinical application of nerve crossing, he soon became displeased with the hypoglossal or spinal accessory crosses because of the associated movements which regularly resulted. The associated movements were so distressing to the patients and persisted so tenaciously as to mar seriously the effect of the operative treatment. Consequently he and his collaborators conducted extensive experiments on more than a hundred baboons, monkeys, dogs, and cats, trying successively all the additional nerves of the neck which could be crossed to the facial nerve, hoping to find one which would produce satisfactory motor recovery with little or no associated contraction (Ballance, 1924–1932). Many of these varied nerve crosses were tried also on human patients. As a result of their extensive experiences, it was finally concluded that the best method of treatment was to avoid nerve crosses entirely and to attempt the more difficult procedure of repairing in the bony canal the damaged facial nerve itself. In one of his latest reports (1932), Ballance stated that we do not know whether the associated movements produced by crossing the facial nerve ever disappear or not. Certainly they regularly failed to disappear after several years in the experimental animals, and their persistence in human patients for many years without any appreciable improvement has been well authenticated.

At the same time there is no question but that some voluntary control of facial movement can be acquired after nerve crossing. It is easy for a patient after crossed nerve regeneration deliberately to lift his shoulder or roll his tongue in order to elicit contractions in the face. To what degree the facial movements can be dissociated by practice is still controversial. It would be expected that, if the muscles supplied by the 11th or 12th nerves could voluntarily be contracted separately under normal conditions, dissociation should be possible as well after the nerves have been crossed to the face. An appearance of gradual dissociation of function is occasionally mentioned. The reports are not at all critical, however, and do not make it clear whether the dissociation is real, or only apparent and achieved by the patient's learning to conceal or counteract with antagonistic muscles the overt movements of the tongue or shoulder. The extent to which voluntary movements, whether dissociated or not, may eventually become automatic and adaptive is another unanswered question. Kilvington (1941) believes that these voluntary movements are possible only when the patient makes a mental effort to move the tongue or the shoulder at the time when facial movement is desired (see also Coleman, 1940). Attempts to imitate facial expression by this means, it is widely agreed, never reach the point where the facial movements become at all natural in appearance. They are always executed with an obvious impairment of spontaneity. Sudden or emotional movement on the normal side of the face is accompanied only by an appearance of full paralysis on the affected side (Phillips, 1938; Kilvington, 1941). Moreover, the facial movements show no variety of expression; the reinnervated muscles always contract en masse (Coleman, 1940) or in abnormal stereotyped patterns, depending on the nerve used and accidents of shunting in nerve regeneration.

Some improvement in the patient's appearance may result from training by the cultivation of a "dead-pan" expression. Both sides of the face then take on a blank expression, and the discrepancy between the normal and affected sides of the face becomes less apparent. This learning to inhibit facial expression is of course quite a different thing from learning to make the deranged nerve connections of the affected side subserve normal function to match that of the normal side. Not infrequently, in the limbs as well as in the face, no movement at all is better than discoordinated movement, and improvement in function may therefore be achieved simply by dropping out the function of the parts involved. For practical as well as theoretical purposes, this negative type of improvement in function after nerve crossing should always be distinguished from any positive central nervous reorganization. Associated movements may also be avoided in a similar negative fashion by deliberate inhibition of the action of the parts originally supplied by the substitute nerve. It has now become customary to instruct patients to practise not positive readjustment, but rather suppression of all facial movements (Coleman, 1940; Cooksey, 1941; Collier, 1941). This is an outcome of a growing conviction that it is impossible to achieve by reeducation any material success in simulating normal facial movements with substitute nerves. Furthermore it has been found that attempts at positive reeducation, far from improving the patient's coordination, will often increase his deformity by exaggerating the facial grimaces and causing them to become habitual.

In summary, the results of crossing the facial nerve in experimental animals and in human patients indicate that very little central nervous readaptation occurs. The reports in recent years have tended more and more to admit the inadequacy of what few voluntary movements are regained, to refer to the permanent persistence of associated movements, and to state definitely that even in the most successful cases there is always a complete lack of any recovery of natural emotional expression. It must not be assumed, however, that this acknowledgment of the failure of the crossed nerves to give up their original central associations and take over new ones suited to their new terminations implies that such nerve cross operations are no longer justified. It is true that whenever possible it is much better to restore function by reuniting the two ends of the facial nerve itself, but when this is impossible, or when it is a matter of relieving facial spasm, nerve crossing may still be indicated because the restoration of muscle volume on the affected side of the face in itself produces a worth-while improvement in facial appearance, particularly when the features are in in repose (Coleman, 1940, 1944b).

Mass movements after nerve crossing

In addition to the association of facial movements with those of the shoulder or tongue after crossing the spinal accessory or hypoglossal nerves to the facial, there is also an association of movements within the face itself. Contraction of one part of the face is associated with contraction of other parts, so that individual movements of the eyelids, lips, or brow on the affected side are impossible. The entire reinnervated musculature reacts much as a unit (Coleman, 1940; and others). This undissociated contraction of the facial muscles after nerve crossing, referred to as "mass movements," "contractions en masse," or "synkinesia," may also be considered a type of associated movement, although of a different order from that which occurs between the face and the shoulder or tongue muscles. Wherever nerves are crossed there arises the problem in recovery of dissociating function not only between the new and old regions supplied by the crossed nerve but also between the various reinnervated end-organs within the new region of distribution.

Such mass contraction or associated movements within the face are due to the fact that the motoneurons of the substitute nerve which previously functioned together continue to do so after being redistributed haphazardly throughout the face, instead of becoming individuated in function according to the different muscles in which they now happen to terminate. Another factor conducive to these mass movements is the multiple branching of regenerating axons, resulting in the linkage of single axons to several different muscles. For recovery of normal function within the face it would be necessary for the original functional organization of the rerouted motoneurons to be completely broken down and the neurons regrouped into new motor pool arrangements according to their common peripheral terminations. Those neurons with branches into more than one muscle would have to be inhibited in all reactions where the different muscles did not function synergically.

This problem of dissociation within the area of redistribution of a crossed nerve has been given little or no direct investigation after nerve crossing in the limbs, either experimental or clinical, although in many of the reports (e.g., Barron, 1934; Bethe and Fischer, 1931) it has been assumed that this type of dissociation had occurred. Estimating the extent of functional dissociation between the new and old areas of supply of a crossed nerve has itself been difficult enough in the limbs; to judge the finer degrees of dissociation within the area supplied by a single nerve would be much more difficult. In the face, however, it is easier to tell whether or not the function of the various muscles is properly individuated, and some evidence on the matter is available.

Undissociated mass movements of the face have regularly been reported after crossing the hypoglossal or spinal accessory nerves to the facial. Cases of which it has been possible to report that these mass movements have gradually given way to individuated function as a result of practice have been rare. These few observations can be accounted for on the basis of (1) trick movements of the eyelids, and (2) incomplete spotty reinnervation of the group of facial muscles and threshold effects, such that with low intensity of contraction only one or a few muscles produce noticeable movements. Dissociation of mass movements within a region supplied by a crossed nerve is presumably more difficult to achieve by learning than is the more gross type of dissociation between the new and old regions of nerve supply. The bulk of evidence is clearly against the possibility of dissociating mass movements in the face. There is no reason for supposing such dissociation to be any more feasible after the crossing of limb nerves.

Mass movements after straight nerve reunion

Since the demonstration by Ballance and Duel (1932) that one can often repair the paralyzed facial nerve by grafting in the facial canal and can thereby avoid the troublesome associated movements that follow nerve crossing, attention has shifted considerably from the problem of reeducation after nerve crossing to that following reunion of the stumps of the facial nerve itself. Although the haphazard shunting of regenerating fibers in the nerve scar after reunion of the two ends of the same nerve creates anatomical confusion and poses a problem of central nervous readjustment, the required adjustment is often of a somewhat different order from that following nerve crossing and has special aspects which deserve separate consideration. Discussion of motor recovery after straight reunion of nerves has been delayed to this point because conditions in the facial nerve and its muscles are particularly favorable for illustrating the problems involved.

There is a great range in the degree to which facial nerve regeneration may result in the formation of atypical nerve connections. In cases where paralysis is caused merely by compression of the nerve, there may be no intermixing or shunting of fibers, so that regeneration leads to restoration of the original terminal connections. Increasing degrees of fiber shunting result from increasingly severe lesions due to infections and other factors. In some cases, therefore, none or only a few of the regenerating fibers may be misdirected, while in other cases of severe infection or complete traumatic severance of the nerve the majority of fibers may be redistributed to foreign muscles. Especially after complete nerve division and the insertion of a graft into the nerve gap, regeneration results in a highly random rearrangement of the normal nerve connections. Since the problem of central reorganization is more important, and the adaptation capacities are more crucially tested in the latter type of case, the following discussion is limited to complete nerve lesions with extensive shunting of fibers into abnormal channels.

Three types of functional disorder have commonly been recorded after regeneration of the completely disrupted facial nerve. First, mass contractions, i.e., inability to individualize the contraction of the various muscle groups. Different facial expressions or separate movement of the lips and eyelids are impossible; the patient can only contract en masse the entire musculature of the affected side of the face—except for the frontalis muscle, which for some reason usually fails to recover any function. Second, facial tics, purposeless brief twitchings of the reinnervated muscles. These tics may be confined to a few muscles or may be present in most of the reinnervated region. Third, contracture of the facial musculature. All the recovered muscles tend to show a sustained active contracture which in some cases may result gradually in a permanent anatomical shortening of the muscles. The contractures become more pronounced when facial expression and tonus is heightened on the normal side of the face.

All three of the above functional disturbances may be attributed to the same fundamental cause, namely, the persistence without central adaptation of the original functional properties of the various facial axons after they have branched and become redistributed at random throughout the array of facial muscles. When, for example, isolated movement of the lips is attempted, the axons originally terminating in the lip muscles are activated, but because these axons have been widely redistributed among the facial muscles there results, instead of separate lip movement, a mass contraction throughout the affected half of the face. When automatic blinking movements of the lids on the affected side would occur normally, the brief flicks of muscle contraction, instead of being restricted to the eyelid muscle, appear in other muscles about the face and are called facial tics. Whenever any muscle would normally be activated all muscles tend to be activated. Every muscle is thus kept in a prolonged state of contraction throughout those periods when any muscle at all would be active under normal conditions. This means that individual muscles get much less chance for complete relaxation and are kept instead in a persistent state of contraction most of the time. Contrasting sharply with these abnormal results of extensive fiber shunting in regeneration are the qualitatively excellent recoveries which follow regeneration after paralyses due to compression in which there is no misdirection of the regenerating fibers.

The mass contractions, facial tics, and contracture, according to most recent reports, are not corrected to any appreciable extent by reeducation. Howe, Tower, and Duel (1937) could see no abatement of tic movements in 27 monkeys with regenerated facial nerves over a period of 2 years. Coleman (1944b) states that normal facial activity is never restored. Ford and Woodhall (1938) cite the case of a patient told to practice before a mirror, in which seven years later all the abnormal phenomena were still present. The history of this case was said to be typical of at least a hundred similar ones in their records. These authors believe that the above phenomena are inevitable in all cases of severe facial palsy and that they persist throughout the rest of the patient's life.

On the other hand, some observers have expressed belief that their patients showed at least slight improvement with practice. Martin (1940), for example, inferred from the improvement observed in two of his cases that the facial tics would probably disappear in a few years. Where functional improvement has thus been reported, however, it is not at all clear whether a positive specific readjustment in the function of the misdirected nerves was indicated or whether the adjustment was simply inhibitory in nature, due to the generalized suppression of the facial centers. Central inhibition of the blinking mechanisms would, of course, eliminate the facial tics. Similarly the complete suppression of all facial excitations should eliminate all three abnormal motor phenomena. The importance of distinguishing between such inhibitory adjustments and positive adaptations of function must be reiterated.

According to more recent views (Collier, 1941; Cooksey, 1941), it is best for patients with motor deformities following facial nerve regeneration to cultivate by practice a "poker face," just as after facial nerve crosses, for there is little or no chance of achieving reeducative adjustments of the positive type. To what extent the mass movements, tics, and contractures can be eliminated by generalized inhibition is still not clear. It is thought at present that attempts to practice positive readjustments usually result only in accentuating the abnormalities. Therefore the reports like those of Ford and Woodhall that describe permanent persistence of the abnormal phenomena may not be applicable to cases instructed from the start to practice inhibition of facial movement rather than positive corrections. For prognosis based on previous case results, it is important to know whether the earlier patients had practiced suppression or positive correction of facial movements.

The permanent persistence of abnormal motor phenomena and the absence of recovery of normal movement after straight reunion are not necessarily proof of the lack of adaptation capacity in the nerve centers. They could be attributed also to excessive branching and misdirection of individual axons, for, so far as is known, dissociation of the action of individual branches of the same motor axon is impossible in mammals by any amount of reeducation. If only a small percentage of axons had branches to separated muscle groups these axons could be inhibited, theoretically, and a good functional result obtained by using only those axons whose branches terminated in the same or synergic muscles. But if nearly all axons had supernumerary branches to separated asynergic muscles, dissociation regardless of central plasticity would be precluded by the peripheral conditions. It must therefore be remembered that lack of dissociation after straight reunion of nerves or lack of dissociation within the area supplied by any crossed nerve may be attributed theoretically to peripheral axon branching as well as to lack of central adaptability.

In this connection it has been demonstrated that a great deal of axon branching may occur in regeneration of the facial nerve (Lipschitz, 1907; Howe, Tower, and Duel, 1937; Ford and Woodhall, 1938), but there have been no pertinent estimations of its proportions in connection with the problem of central reorganization. Howe, Tower, and Duel (1937) attributed the common abnormal motor results of facial nerve regeneration primarily to axon branching and suggested that reeducation within the facial nucleus probably would correct what abnormalities might otherwise result from fiber misdirection without branching. Collier (1941) is of the opinion that normal dissociated movements after recovery tend to predominate over the abnormal mass movements. This might be taken as a sign in favor of the idea that reeducation corrects the function of all but those fibers with supernumerary branches. On the other hand, it might mean merely that redistribution of regenerated fibers has not been entirely random, that due to incompleteness of the nerve lesions, good orientation of the nerve stumps, or possibly unknown factors favoring retention and maturation of normal over abnormal connections there has been a statistical predominance of normal terminations. Spiller (1919) and Ford (1933) ascribed mass movements and contracture to fiber misdirection alone, with no emphasis on axon branching. Pertinent information on this issue could be obtained by crossing cleanly two branches of the facial nerve. This should produce associated movements within the face, caused by misdirection of facial fibers, but without axon branching between the two muscle groups involved. If readjustment within the facial nucleus is possible, it should occur under these conditions. Such an experiment was undertaken by Fowler (1939). He crossed reciprocally in a "series" of monkeys, two branches of the facial nerve, one supplying the lower lip and the other the eyelid muscle. The signs of partial denervation gradually disappeared completely. No tic or associated movements developed. However, no anatomical check was given to determine whether the cross-sutures had been successful. In two other monkeys the same nerve branches were crossed only one way, that to the eye being crossed to the distal stump of the nerve to the lips. One-way crosses of this sort are technically much easier, and the chances of the sutures being successful are greatly increased. Also, reeducation under these conditions would presumably be less difficult, since only a simple one-way adjustment is required instead of a reciprocal rearrangement. In both of these two animals, however, nerve regeneration resulted in associated tic-like movements of the lip synchronous with eyelid movements on the normal side. Once established, this abnormal "blinking" of the lip remained constant over 8 months, as long as the animals were observed. In these animals lip movement of normal character had already returned in as early as 10 days after nerve section, and the eyes could again be completely closed after 4 months, although no new innervation to the eyelid muscles had been supplied. Since both functions were recovered, without reinnervation, the recoveries cited above after reciprocal crosses may similarly have occurred independently of any crossed innervation. In contradiction to the more reliable portion of his own evidence, Fowler oddly drew the conclusion that when nerve bundles are rerouted, reeducation takes place so that no association or tic-like movement occurs. He maintained that tic-like and associated movements are caused not by improper rerouting of nerve branches but by splitting of axons in the neuroma. Clearly the experiment should be repeated.

It may be said in summary that the question of how much the lack of positive reeducative adjustment after facial nerve regeneration is attributable to axon branching and how much to lack of central plasticity remains unanswered. This problem is of more than theoretical interest. From the standpoint of the micro-mechanics of nerve regeneration and repair, the branching and the misdirection of fibers are two different things. It might well be possible, for example, in many cases to reduce axon branching to a minimum even though considerable fiber misdirection be inevitable. This would be a worthy achievement, if it were certain that unbranched misdirected fibers are easily adapted in function to suit abnormal terminations.

The oculomotor nerve supplies an array of muscles the differential function of which, as in the case of the facial muscles, is relatively easy to analyze. Functional recovery after regeneration of the oculomotor nerve has been described by Bender and Fulton (1938) in a chimpanzee, and by Bender and Alpert (1937), Bielschowsky (1940) and others in man. Undifferentiated mass action of all muscles supplied by the nerve has been observed just as after facial nerve regeneration, and has been attributed to the same cause, namely, the disorderly regeneration of axis cylinders into the distal nerve stump and consequent disarrangement of normal terminations. The chimpanzee was not retained to find out if reeducative correction could be achieved, but in a human patient Bender and Alpert found all the characteristic motor abnormalities still present seven years after the paralysis had been inflicted. In general nature, the immediate and late results of oculomotor nerve regeneration have been described as being identical with those of facial nerve regeneration.

Motor abnormalities after straight nerve reunion are not so easily detected in the limbs, for reasons already stressed. In many of the older clinical accounts of recovery after straight nerve regeneration, it was assumed that reeducation could and did smooth out the motor deficiencies which otherwise should follow the misdirection of motor fibers. There has been a growing tendency, however, to acknowledge more fully the qualitative shortcomings of nerve repair, and there seems, on the basis of the more recent descriptions, little reason to believe that the late functional results of straight nerve regeneration in the limbs are essentially different from those obtained after regeneration of the facial and oculomotor nerves. The summary reports of Swan (1918), Thorburn, Sargent, Forrester-Brown, and Joyce (Thorburn, 1920a, b), Buzzard (1921), and Bristow (1941), among others, indicate that qualitative motor defects due to fiber branching and shunting in straight regeneration of limb nerves in man are of regular occurrence. Mass action and the development of permanent contractures have been described. It is commonly recognized that recovery is best after regeneration of nerves whose fibers are relatively homogeneous in function, like the radial nerve. Lack of readjustment would, of course, be the less noticeable, the more homogeneous the functional content of the nerve. Recovery is poorest after regeneration of nerves like the median, which supplies many small muscles that normally function in complex differentiated combinations and in which the failure to recover dissociated action produces a distinct handicap. In the more heterogeneous nerves there is a marked contrast between the qualitatively excellent recovery that follows regeneration after mere compression with no shunting, and the qualitatively poor recovery that follows full severance, even though in the latter case regeneration may be quantitatively good (Buzzard, 1921; Gutmann and Guttmann, 1942; Berry, Grundfest, and Hinsey, 1944). It is not infrequently acknowledged that the more refined and complicated coordinations are never recovered after regeneration of severed limb nerves. Ford and Woodhall (1938) describe persistent contraction en masse of the muscles supplied by the ulnar nerve five years after its regeneration in man. Although recovery was quantitatively good, sufficient dissociation of muscle function to fasten buttons was still unattainable. The picture of the results of nerve regeneration in the limbs is on the whole definitely less clear and less well authenticated than that for the face, but the foregoing suggests that the possibilities and limitations of reeducation are not essentially different in the limbs.

Recovery after severance and regeneration of a nerve is therefore probably never complete in a qualitative sense, due to fiber misdirection. Complete recovery could be expected only if all the nerve fibers were strictly homogeneous, but even in the radial nerve this is far from being true. It is further questionable that even the somatic motor fibers of a nerve branch to a single simple-type muscle are truly homogeneous. There are suggestions from the histological and physiological work on muscle and its motor units (Denny-Brown, 1929; and others) that different fibers may have different properties with respect to the size of the motor unit supplied, its location in the muscle, the central threshold of excitation at which it fires, the frequency range of discharge, the type of muscle fibers supplied with respect to their speed of contraction, and their resistance to fatigue. Thus it may be that the somatic motor fiber supply of a simple muscle is quite heterogeneous when examined in detail, and that accordingly the normal function of the muscle depends upon some orderliness in the termination of the different motor axon types within the muscle. Random redistribution of the motor axons of a single muscle would not be expected to lead to any gross temporal displacement of the action phase of the muscle, but one would predict disturbance in the control of fine gradations of intensity of contraction, disturbance of the incidence of discharge for low intensities, decreased strength, and decreased resistance to fatigue. Similar disturbances would, of course, be expected also in increased degree after regeneration of nerves containing several muscular branches. Such motor defects have not been searched for particularly. It is occasionally mentioned (Perthes, 1922; Stracker, 1919; and others), however, that reinnervated muscles remain far below normal both in strength and in resistance to fatigue, although they have recovered approximately their original volume. To what extent such disturbances may be indirectly caused also by misdirection of sympathetic or sensory fibers is not known.

Comparison of results in face and limbs

Others have been impressed by the pronounced contrast between the persistent abnormal mass and associated movements regularly following nerve regeneration in the face and the excellent recoveries of normal function often reported in the limbs, particularly after experimental nerve crossing. The contrast is all the more striking when it is remembered that in man the motivation for correction and concentrated efforts at reeducation of facial distortions has been much stronger than with disturbance of limb coordination. Although recent observations (Ford and Woodhall, 1938; Sperry, 1940–1943; Watrous and Olmsted, 1941; Obrador, 1942a, b) have tended to erase the contrast, it still requires comment. Barron (1934) attempted to account for the difference on the basis of the smaller ratio of sensory fibers in the cranial nerves. Other hypotheses could easily be advanced, but the evidence when weighed suggests that the discrepancy between functional readaptation in the face and in the limbs is probably in large measure more apparent than real, that the motor abnormalities have been essentially the same in both regions but that in the limbs they have been better concealed and compensated for by the subjects, and less easily detected by the observer, less attentively and less accurately recorded.

Results of Crosses Involving Miscellaneous Somatic Motor Nerves

There are a few reports on the crossing of somatic motor nerves not included in the limbs or as substitutes for the facial nerve.

Rawa (1885) crossed the central end of the divided hypoglossal nerve of the tongue to the distal end of the divided vagus in a variety of mammals. After allowing time for recovery he transected the other vagus nerve. Although most of the animals died shortly afterward, as if both vagi had been cut, survival was sufficiently long in some cases to suggest to Rawa that the crossed hypoglossus was transmitting effective impulses. The absence of any check, to insure that the central vagus stump had not reestablished connections, or that merely a recovery of volume and tonus in the laryngeal muscles or atrophy of these muscles (Schafer, 1919) would not in itself prolong survival, renders these cases inconclusive.

Calugareanu and Henri (1901) crossed the central end of the hypoglossal motor nerve in the dog to the distal end of the lingual nerve of the tongue, in which nerve run autonomic efferent fibers to the salivary glands. After regeneration, salivation on the operated side was about five times as profuse as on the normal side. Since both hypoglossal and salivary fibers are excited together during eating, no temporal disarrangement was to be expected. No adaptation in the intensity of reaction was mentioned. One-third of the hypoglossal was sutured to the distal end of the chorda tympani by Glasson (Anokhin, 1935) in dogs, but the quantity of salivation after recovery in these cases was never as great as normal.

Erlanger (1905) crossed the hypoglossal nerve, and in other cases a stump of the brachial plexus, to the distal end of the vagus in dogs. He found no evidence of any restitution of normal innervation of any of the organs to which the vagus is distributed except the heart. He observed in one or two of his five dogs some reflex effects on heart rate associated with respiration and with electrical stimulation of afferent nerves, and he concluded that regenerated fibers of spinal nerves may serve as the efferent path of cardiac reflexes associated with the act of respiration and of reflexes started by electrical stimulation of afferent nerves; and that through these fibers the central nervous system may exercise a tonic inhibitory control over the heart. In one case he felt that there was some evidence that the inhibitory center of the heart had actually shifted to the nucleus of origin of the crossed spinal nerve. The evidence in his cases was admittedly extremely meager, and the few results recorded do not necessarily indicate any shift of central nervous integration.

The anterior root of the phrenic nerve was crossed to the distal stump of the cervical sympathetic trunk in cats by Cannon, Binger, and Fitz (1914, 1916). This was done for the purpose of delivering a volley of impulses to the superior cervical ganglion every time the animals breathed. Four animals which survived the regeneration period developed marked symptoms characteristic of exophthalmic goiter in man, including tachycardia, hypernormal metabolism, hypernormal excitability, respiratory hippus, exophthalmus, loose bowels, falling hair, dilatation of pupil on the operated side, and hyperplasia of the adrenal glands. The animals died within three months of the first appearance of the symptoms, except for one case in which the thyroid gland on the affected side was removed. This animal lived normally until purposely killed seven months after the thyroidectomy. It may be said that the animals died because the discharge of the crossed phrenic nerve fibers failed to become adaptively modified to suit the new peripheral connections. Attempts by others to obtain these results (see Burget, 1917; Marine, Rogoff, and Stewart, 1917), however, have been unsuccessful.

Efforts have been made to restore function to paralyzed vocal cords by substituting a nearby healthy nerve for the paralyzed recurrent laryngeal nerve (Hoessly, 1916; Colledge, 1925; Blalock and Crowe, 1926; Colledge and Ballance, 1927, 1928). The central stump of the vagus, phrenic, or descendens hypoglossi nerves has been united to the distal end of the divided recurrent laryngeal nerve in experimental studies on goats, dogs, monkeys, and baboons, and Hoessly inserted a branch of the spinal accessory directly into the laryngeal muscles in the dog. Because of the location of the vocal cords, observation of natural movements has been restricted to the rhythmic adduction and abduction of the vocal cords in tranquil breathing under light anesthesia. When the intrinsic laryngeal muscles were reinnervated by the vagus, spinal accessory, or descending hypoglossal nerve, the tone of the muscles was restored, effecting some improvement over the paralyzed condition, but there was no recovery of normal respiratory movements (Hoessly, 1916; Colledge, 1925; Colledge and Ballance, 1927). Colledge attributed this to the lack of an adjustmental shift in the central timing of the discharges of the crossed nerves. He suggested that if the vocal cords could be observed under other conditions, one would find abnormal associated movements of the cords, for example, during swallowing after use of the descending hypoglossal. When the phrenic nerve was used, rhythmic movements of the cords in quiet respiration were often recovered, but this is because the phrenic impulses are normally associated in breathing with those of the recurrent laryngeal nerve, so that no central nervous dissociation was required. The timing was not perfectly accurate after reinnervation by the phrenic, however, and sometimes incoordination amounting to a complete reversal of abductor and adductor movements resulted. When the animals became excited, incoordination produced stridulent respiration. There was no indication that such incoordination of the automatic movements of the vocal cords supplied by the phrenic nerve was ever corrected by reeducation.

One might expect that reeducation would be easier in the case of the more voluntary movements of phonation in human patients. In 10 patients in which satisfactory anastomosis of the descending hypoglossal to the recurrent laryngeal was performed, Frazier and Mosser (1926) describe the results as "failures" in 4 cases, "improved" in 5, and 1 (unilateral paralysis) "recovered." Judging from the conspicuous avoidance of the problem of recovery of motor coordination in this report after its previous anticipatory introduction (Frazier, 1924), and from the references to this work by Colledge (1925) and Ballance (1924), it appears that the results were not satisfying in this regard. Another case in which the phrenic was tried is also mentioned, without any details of the pattern of the recovered laryngeal movements.

Ballance (1924) reported a surprising instance in which normal contractions of the diaphragm were restored after its reinnervation by the descending hypoglossal nerve, but he adds a cautionary footnote saying the observation needs confirmation by further experiment.

With the specific purpose of testing the readaptation capacity of the central nervous system, Cordero and Carlson (1927) crossed the anteriormost root of the phrenic nerve to the distal end of the nerve to the sternohyoid muscle in 5 dogs. Regeneration was successful in 4 cases, with the result that the sternohyoid muscle showed contractions synchronous with each inspiratory act and proportional in intensity to the depth of respiration. These contractions were very weak and could not be distinguished until the muscle was exposed through the skin. There was nothing to indicate any shift in the respiratory center toward modifying or dividing its discharges so as to eliminate the abnormal, superfluous contractions of the sternohyoid. The animals were kept three to six months after operation, but no sign of readjustment was noted in any of them.

Results of Crossing Autonomic Nerves

When the central stump of an autonomic nerve (Ranson's terminology) is made to reinnervate foreign end-organs by nerve crossings, readjustment frequently necessitates reorganization of central nervous patterns which normally are of an involuntary or automatic nature. It may be difficult or impossible to separate so-called voluntary and involuntary activities; nevertheless, there are extremes of behavior to which the terms have been applied, and the possibility of there being a difference between them in reeducability after nerve crossing is worth noting. It is commonly assumed that the greater the degree to which a given reaction or activity is subject to voluntary control, the easier should be reeducative correction after crossing nerves mediating the activity. The glandular and smooth muscle responses governed through the autonomic system are in general less subject to voluntary regulation than are skeletal muscle responses, and therefore one would expect to find less evidence of central nervous reorganization after crossing autonomic nerves than after crossing somatic nerves.

Rawa (1885) crossed the central end of the divided vagus nerve to the distal end of the hypoglossal in several different mammals and inferred that normal tongue movements can be effected through the crossed vagus. His experiments have been criticzed on the basis that insufficient care was taken to prevent reestablishment of original connections (Langley and Anderson, 1904b; Erlanger, 1905). Rawa's report induced Schiff (1885) to repeat the experiments. He crossed the central end of the vagus to the hypoglossus in 5 dogs, being careful to excise widely the two uncrossed stumps. No return of normal tongue movement was found. Instead, rhythmic movement correlated with vagal functions began to appear between the 11th and 16th weeks after operation. Reichert (1885) made a thorough examination of Schiff's dogs at six months after operation. At this time there was still no sign of normal movements on the affected side of the tongue; only abnormal tremors associated with various actions of the vagus occurred. Isolated areas of the tongue showed rhythmical contractions, some associated with inspiration, others with expiration. Coughing and deep breathing accentuated these reactions. Other tremor movements were found associated with swallowing and vomiting. Thus the various types of vagus fibers which had made connections with the tongue musculature had retained their original central timing, and there were no indications of any adaptive shift to suit the new peripheral connections. The failure of the intrinsic laryngeal muscles to recover normal function after reinnervation by the vagus has already been mentioned.

Langley (1898b) crossed the vagus nerve to the rostral end of the divided cervical sympathetic trunk in 6 cats. After their recovery, he noticed that whenever the cats were lapping and swallowing milk there was an associated retraction of the nictitating membrane of the eye on the operated side, and also a constriction of the ear arteries and a dilatation of the pupil. On one cat whose anger was easily aroused the nictitating membrane would pass halfway over the eye whenever the animal was teased. The membrane gradually returned to its customary state as the animal became calm. The pupil on the operated side tended to constrict during fits of anger instead of dilating, as did the normal pupil. The foregoing symptoms were observed repeatedly and became more marked with the passage of time. These abnormal associated responses indicate a lack of any central nervous readjustment. They persisted as long as the animals were kept, which, however, was at the most only 123 days. Langley also crossed the lingual nerve containing the vasodilator and secretory fibers of the salivary glands to the rostral stump of the cervical sympathetic trunk in one cat. He observed, beginning on the 53rd day after operation, that the act of taking milk regularly caused a contraction of the arteries of the ear on the operated side. Nerve impulses normally conducted to the salivary glands had become rerouted to the arteries of the ear. Their timing remained associated with salivation without an adaptive shift to suit the new termination of the fibers, but again the animal was kept only 71 days after operation.

The central end of the vagus nerve in the dog was sutured to nerves of the forelimb, usually the radial, by Anokhin (1935a, b, 1936a) and his coworkers. They reported that after regeneration the forelimb muscles reinnervated by the vagus came to function in coordination with the other forelimb muscles in locomotion as well as in withdrawal responses conditioned to a bell. Moreover, stimulation of a specific area of the motor cortex elicited contractions of the reinnervated muscles along with the intact muscles of the forelimb. It was concluded that the intracentral connections of the vagus nucleus change radically as a result of the anastomosis and somehow enter into association with the forelimb motor centers of the cortex. Published along with this study in the same monograph are later studies, in which the same operation is said to result in contractions of the reinnervated forelimb muscles clearly associated with respiration and deglutition. In fact, the action of the forelimb muscle supplied by the vagus is described as a delicate indicator of the exact state of tonus of the respiratory center. All changes in respiration are very closely reflected in the forelimb muscles, and the phenomena are so illustrative and constant that they were used for lecture demonstrations. Further study revealed that the "breathing and swallowing" movements of the forelimb were mediated entirely through the recurrent laryngeal fibers. The results of crossing the vagus nerves, including the recurrent laryngeal fibers, into the forelimb are thus given on the one hand as demonstrating extensive central nervous readaptation, while in other reports they are said to the contrary to demonstrate with striking clearness complete retention by the crossed motor fibers of their original central relations and functions. Such puzzling contradictions are not rare in Anokhin's monograph.

Ballance (1931) crossed the central end of the divided cervical sympathetic trunk to the distal end of the facial nerve in cats, dogs, and monkeys. He mentioned no abnormal associated movements following these crosses, nor did he mention any voluntary coordinated movements or emotional responses. He also crossed the central cervical sympathetic nerve to the distal hypoglossal nerve but again remained noncommittal about the recovery of coordinated movement, except for the remark that when the mouth was opened the tongue retracted, and both sides appeared to move together.

Although various "trophic" effects due to interruption of autonomic fibers have been described after spinal nerve lesions (Stiles and Forrester-Brown, 1922; Meige and Bénisty, 1916), the problem of the quality of recovery of the different autonomic functions in relation to fiber misdirection remains to be studied.

After regeneration of the facial nerve in man, particularly when the lesion is proximal to the geniculate ganglion, there may result, in addition to the inevitable abnormal mass movements and contracture of the striated musculature of the face, abnormal autonomic phenomena. The syndrome known as "crocodile tears" (Kaminsky, 1920; Kroll, 1929; Ford, 1933) is such. This is excessive lacrimation on the affected side whenever the patient eats or takes any sapid substance into the mouth. Even appetizing odors may cause lacrimation. In other words, whenever salivation occurs, there also results an associated copious flow of tears from the eye on the side of the regenerated nerve. This has been attributed to the aberrant regeneration of salivary secretory fibers into the lacrimal glands of the eye, instead of into the salivary glands where they originally terminated. The central timing of these aberrant fibers remains unadjusted to their new terminations, with the result that tears are produced when salivation is called for. Correction by central nervous readjustment apparently fails to occur (Ford and Woodhall, 1938). Ford (1933) reported a case in which the associated lacrimation had already persisted sixteen years when first observed.

Of similar nature is the "auriculo-temporal syndrome" (Fridberg, 1931; Ford, 1933; Ford and Woodhall, 1938), which not infrequently follows damage and regeneration of the auriculo-temporal branch of the 5th nerve. After nerve regeneration the anesthetic area of skin over the temple comes to show paroxysmal sweating and vasodilation whenever salivation occurs. At other times the skin in this area is indistinguishable from normal skin. This phenomenon, like "crocodile tears," also has been attributed to the misdirection of salivary nerve fibers. The secretory and vasodilator fibers of the parotid gland apparently misregenerate to the sweat glands and blood vessels of the skin. In these cases also, the profuse sweating and flushing of the temple whenever the patient eats has persisted without signs of correction by central nervous adjustment. A patient in whom localized flushing of the skin with excessive sweating in the region underneath the chin on one side of the throat was always associated with salivation was reported by Uprus, Gaylor, and Carmichael (1934). They ascribed the phenomenon to misregeneration of salivary fibers following an incision in the right side of the neck. The patient was 22 years old at the time of observation and the dysfunction had been present since the age of seven.

It is possible that the abnormal associated phenomena described above were due to the presence of supernumerary branches of single salivary axons, as well as to their misdirection without branching. Even if axon branching were present, however, the distressing phenomena could at least have been inhibited theoretically by complete suppression of discharges to the salivary gland involved or to the salivary glands on the affected side of the face. Such central dissociation of function should be simpler than a dissociation at the cellular level, calling for excitation of some cells of the salivary nucleus with inhibition of those with abnormal peripheral termination. The fact that not even some such generalized inhibition of the salivary nucleus was achieved in the above cases is significant. The best the patients could do, apparently, was to learn to swallow food very quickly or to use food that did not stimulate salivation (Ford, 1933).

To summarize, the observations on functional recovery after misdirection of autonomic motor fibers, except for the report of Anokhin and Ivanow which is contradicted by further studies in the same laboratory, indicate that aberrant motor fibers have continued to function in their original manner and have not acquired, either in man or in animals, new central associations suited to the new end-organs.

FUNCTIONAL RESULTS OF MUSCLE TRANSPOSITION

After the transposition of muscles or their tendons as well as after nerve crossing, readjustment is required in the central timing of motor impulses in order to restore normal muscular coordination. The timing of a muscle's contraction in various movements must of course be adapted to the mechanical action of the muscle. If the mechanical action is changed by transplantation, then the central firing of the motoneurons of the muscle must be shifted to correspond with the normal action phase of whatever muscle the transplant is substituted for; otherwise coordination would be disrupted. The central reorganization required after muscle transposition, however, is usually of a quite different order from that required after nerve regeneration. When a muscle is transposed with its innervation intact, recovery of correct function demands only dissociation and reassociation of functional relations between the intact "motor pool" of the transposed muscle as an organized unit and the remainder of the organized central system. After reunion or crossing of heterogeneous nerves, on the other hand, the haphazard reestablishment of individual nerve connections regardless of previous functional groupings makes necessary a complete breakdown of the original central organization of the elements involved and a thorough reorganization starting at the neuron level. It follows that reeducation should be easier after transposition of muscles than after nerve regeneration.

Transposition of Limb Muscles

Experimental

Manigk (1934) observed that frogs in which the hind legs had been sutured together down to the ankle walked exactly the same after their gastrocnemius muscles had been reciprocally transposed as when these muscles were left uncrossed. He attributed this to instantaneous reorganization of coordination patterns and emphasized the role of peripheral mechanisms in shaping central integration. The experiments were soon repeated and extended by Taylor (1936), who showed that Manigk's conclusions were erroneous because the recovered movements proved to be entirely passive and even persisted after denervation of the crossed muscles. Furthermore, when Taylor made the plantar extensor gastrocnemius muscle into a dorsiflexor in the same leg, reversed movements resulted so that dorsi-flexion occurred when the foot normally would have shown extension. The experiments showed that no immediate spontaneous reorganization follows transposition of these muscles in the frog. The animals were not kept to find out if any reeducational adjustment might occur with experience and practice. It has been demonstrated by Weiss (1937b), however, that after reorientation and transplantation of entire limbs into such positions that normal coordination is either useless or detrimental, urodele amphibians continue to use the old motor coordination patterns indefinitely without any sign of correction by learning.

Laptev and Anokhin (Anokhin, 1935a), after transplanting part of the lateral quadriceps muscle to a flexor position in the hind leg of the cat, concluded on the basis of the appearance of leg movements in locomotion that the transplanted extensor had changed its function to that of a flexor. When the muscle after 5 months training was isolated for kymograph recording, however, the transplanted portion contracted synergically with its counterpart as a normal extensor. The results were interpreted as being due to a "dynamic rearrangement" in central nervous relations without any fixed change. Because the action of the transplanted portion of the quadriceps in locomotion could easily have been masked by the function of the remaining musculature of the thigh (see J. E. Stewart, 1925; D. Stewart, 1937), the assumption that readjustment had occurred in these cases is not justified.

Transposition to an antagonist position of a dorsi-flexor or a plantar-extensor muscle of the shank in dogs and cats was accomplished by Watrous and Olmsted (1940) in five animals. Their results were the same as Anokhin's. No incoordination in locomotion was evident as a result of the operations, but when the animals were decerebrated and the transplanted muscles were isolated and prepared for kymographic recording, it was found that their reflex activity under these conditions was the same as if transplantation had not been performed. Absence of readjustment after decerebration cannot, of course, be taken as proof that no reeducation had occurred.

It had already been shown (Sperry, 1939; 1940) that in the rat a clear-cut reversal of flexor and extensor movements results after reciprocal transposition of dorsi-flexor and plantar-extensor muscles, provided care is taken to abolish the normal action of associated muscles which might otherwise obscure the action of the transplants. When dorsi-flexion is called for, the transplanted dorsi-flexor contracts producing extension, and vice versa. This definite reversal of foot action was found in all activity, in slow deliberate voluntary movements as well as in reflex responses. Moreover, it persisted without any correction by central reorganization. Control animals in which the nerves of the transposed muscles were also crossed demonstrated that the transposed muscles were quite capable of producing flexion and extension in the correct phase of leg movement if, as was here provided by crossing the nerves also, the central discharges to the muscles were correctly timed. It was obvious that no foot movement at all would have been more advantageous to these animals than the reversed movements and yet, even after amputation of the forelimbs or under special training conditions, the rats not only failed to adapt the central discharge pattern to the rearranged muscle action but failed even to inhibit the maladaptive reversed movements.

It was also found that reversed movements of the elbow in the forelimb of the rat result after transplantation of the flexor and extensor muscles of the upper arm (Sperry, 1942a). Different types of muscle translocation were performed. In some cases the transplantation was made in only one direction, i.e., a flexor was transposed to serve as an extensor, and all other brachial muscles were excised. In other cases reciprocal transposition of flexor and extensor muscles was performed. In a third series, one flexor muscle was left in normal position, and another transposed to act against it. A certain type of trick movement featured prominently in the results, but in none of the different series did the transposed muscles come to take over new function suited to their new mechanical effect. Electromyographic and motion picture analysis revealed that the transposed muscles were still contracting in their original uncorrected action phase after prolonged training under conditions conducive to reeducation.

There is no question but that under these conditions of reciprocal muscle transplantation, where the rat failed to make an adaptive adjustment in the action of the test muscles, man would readily be able to do so in some degree. It would merely be necessary for man to make a mental effort to flex the foot when he wished actually to extend it, and vice versa. To what extent such deliberative corrections could eventually become rapid, automatic, and generalized, so as to transfer readily to unpracticed activities, can only be guessed at present.

Clinical

In clinical practice, clear-cut reciprocal transplantations with excision of other muscles, as in the experimental cases above, are of course never encountered. The problem of functional dissociation and reorganization after transposition of one or two muscles in one direction only, with associated muscles of various functions left intact, as is generally the situation in human patients, is one of greater complexity. Clinical accounts of the functional results of muscle transposition are far too numerous to permit their separate consideration and discussion. As a rule, just as with the observations of recovery after nerve crossing, recovery in man has been viewed from a practical unanalytical standpoint, without much attempt to determine critically the extent to which the central timing of muscles can be shifted to suit new mechanical relations (Leveuf and Perrot, 1937). Opinions which have arisen from general clinical experience are by no means unanimous. Some authors have held that the nerve centers are very plastic and are readily adapted to bring about coordinated movements after antagonistic transplants (Codivilla, 1904; Perthes, 1918; Billington, 1922; Bethe and Fischer, 1931). Other workers have warned specifically against attempts to make muscles serve entirely new and antagonistic functions and state that many failures follow the use of antagonistic muscles for transposition, because of the inability of the transposed muscles to revise their function to suit a new action (Steindler, 1919, 1940; Dunn, 1920; Gill, 1921). The type of transplantation most frequently undertaken in man and most consistently successful is the transposition of forearm flexors to serve as extensors after radial nerve paralysis. The claim that the function of muscles can easily be reversed has been based in no small degree on the results of this classical transplantation to correct wrist drop. It has been pointed out, however (Stiles and Forrester-Brown, 1922; Steindler, 1940), that the transplanted muscles in such cases do not take on an entirely alien function, since the flexor and extensor muscles in this region show a great deal of co-contraction in normal activities. Also there is a pronounced benefit simply from the improvement in muscle balance, so that it is questionable to what extent good recovery in these cases can be considered evidence of central readaptation.

It is generally agreed that muscle transposition very often leads to functional improvement, but this does not imply agreement regarding the effectiveness of reeducation. Stiles and Forrester-Brown (1922) state that although it is possible that an antagonistic muscle can never be trained to work independently of its old group in support of its new one, the results of antagonistic transplantation may nevertheless be beneficial. Improvement in function may be due to a number of factors. Trick movements, improvement in muscle balance about a joint by subtraction from the strong side as well as by addition to the weak side, provision of an elastic opposition for the intact healthy muscles to work against, unspecific stabilizing effect on a joint, natural synergic action of the transplant with the muscle for which it is substituted, among other factors, may all lead to functional improvement in addition to central readaptation in the timing of the transposed muscles. To exactly what extent this latter factor itself can be counted on to aid in recovery is not clear from the varying opinions that have arisen from gross clinical observation.

Even those attempts to approach the problem critically with the use of special methods for detailed analysis of the contraction patterns of the muscles involved have not yielded consistent conclusions. The most persistent effort to determine in a thorough manner the effects on motor coordination of muscle transplantation has been made by Scherb (1928–1938). According to his conclusions, reeducation occurs readily after the transposition of arm muscles. So far as it is surgically possible, any arm muscle may be substituted for any other with the expectation that the function of the transplant can be shifted to suit the new position. In the leg also, complete readjustment is possible, except under certain special conditions as follows: When the paralyzed group of muscles for which an antagonistic muscle is substituted is not completely paralyzed, the remaining functional portion, even though it be the merest remnant, will prevent readjustment in the function of the transplant in automatic walking movements. Adjustment will still be possible in simple voluntary movements, however. Scherb emphasizes strongly the difference between simple voluntary movements which the patient is asked to perform while at rest, and the automatic involuntary act of walking. Ability to use a muscle correctly in a simple deliberate movement is no guarantee that the muscle will also work correctly in involuntary reactions. Scherb also opposes definitely the once common notion that the function of a transplanted muscle is shifted immediately and spontaneously in adaptation to its new action, without any training. Considerable practice, he has found, is necessary to reverse the function of a transplanted limb muscle. Scherb's opinions and general rules for muscle transposition, as far as they go, have been widely accepted (Leveuf and Perrot, 1937).

Several investigators have studied experimentally the function of the flexor biceps femoralis muscle after its transplantation to serve as an extensor of the knee in place of the paralyzed quadriceps. In this one case, at least, we have the advantage of independent opinions based on observations in different laboratories. Vinke (1934) studied the action of these muscles in locomotion with the aid of his myokinesiometer. He concluded, on the basis of admittedly few cases, that muscles retain their original or nearly their original contraction phase after transplantation. He pointed out, however, as have also others (Stiles and Forrester-Brown, 1922; Scherb, 1938), that the normal contraction phase of the hamstring muscles is multivalent and is such as to make these muscles of some service in the transplanted position without any change of their normal timing. Some improvement in the use of the limb thus results without any central readjustment. For this same reason Scherb, who also had studied the action of the transplanted hamstrings, did not consider the failure of these particular muscles to give up their original contraction phase as an exception to his principles for functional readjustment. Dunn (1920) mentioned that in his experience transplantation of the biceps to the quadriceps had not resulted in voluntary control of knee extension. Porter (Gill, 1921) also stated that he had never yet seen a transplantation of the hamstrings to replace the quadriceps which was satisfactory. Tubby (1906) and Ritter (1928) were more optimistic in opinion, however, while Weiss and Brown (1941), using electromyographic methods to record action of the transplanted biceps femoris, found a definite adaptive shift in the timing of the transplant from the flexor to the extensor phase in various types of movement. They reported temporary relapses into the old flexor association, however, even years after operation. The above contradictions regarding the possibility of functional readjustment which have arisen about this one type of muscle transplantation that has been most intensively analyzed serves to illustrate the complexity of the problem in man and the lack, as yet, of any complete understanding.

On the whole it may be inferred from the literature that with practice man is capable of dissociating the action of individual muscles from associated muscles so as to adapt the action of a transplant to its new position in at least the simplest voluntary movements. This is easier in the arm than in the leg. The problem after muscle transposition in man is not so much "is any readaptation possible?" as "to what extent is readaptation possible?" Readjustment apparently is not automatic but depends on the learning process, and consequently is more apt to be found in slow, practiced, simple, deliberate, voluntary movements than in rapid, unpracticed, complex, involuntary, surprise reactions. Although most studies and observations have been confined to movements of the former type, some of the studies, cited above, indicate that readaptation of transplanted leg muscles is possible under some conditions in the automatic walking coordinations. The walking coordination recovered by most paralytics after muscle transposition, however, usually resembles little the smooth gait of the normal person, and to picture the transplanted muscles serving in the place of their antagonists in a thoroughly efficient manner in the natural automatic walking movement is to get an erroneous impression of the recovery.

Between simple deliberate movements, on the one hand, and the automatic movements of locomotion on the other, and extending beyond these limits, there is a manifold range of different types of motor coordination, varying greatly with respect to complexity, speed, amount of previous practice, and other factors. The function of transplanted muscles throughout most of this possible range of activity has remained unexamined. That a person after practice could use a transposed flexor to extend his fingers for demonstration does not mean the transplant would work properly in piano playing or even in the many simpler everyday performances which involve habitual and automatic extension of the fingers at the proper time, with the proper speed, and in the proper degree. The extent and ease of readjustment may be expected to vary greatly with different types of performance.

The readjustment problem may be expected to vary also with different muscles transposed, not only with respect to whether they are in arm or leg, but also in accordance with the degree of functional dissociation to which the muscles are subject under normal conditions and in accordance with the nature of the normal functional interrelations between the transplant and whatever muscle it replaces. Relations of intensity of contraction must be considered, as well as relations of timing. After transplantations involving anatomical antagonists which normally show considerable cocontraction, the required adjustment may be primarily one of intensity. These functional interrelations of muscles with their associated groups and with the group for which they are to substitute will be different for different types of performances, so that these variables are not really separable from those of the preceding paragraph but merely constitute further dimensions in the manifold range of readaptation requirements. In summarizing the literature it can only be said that although some of the reports imply that readaptation, particularly in the arm, may approach completeness, there is as yet very little actual evidence of the extent to which readjustments may go.

Whereas the rat fails to dissociate and readapt as a unit the function of muscles moving one limb joint, man is capable of dissociating and readjusting the function of individual muscles. In regard to this marked human superiority, the great difference between man and the lower mammals in the degree of differentiation of muscular coordination patterns which exists normally is worth noting. In the quadrupeds the limbs are used in a comparatively stereotyped manner. They tend to be flexed or extended as a whole, without differential movements at the various joints. In some cases the limb structure itself tends to prevent differential movements. For example, flexion of one joint at the same time as extension of a neighboring joint may be precluded by the short length of multiarticular muscles and their tendons. Because of the differences between man and the quadrupeds in the normal degree of dissociation of muscle function, the problem of central nervous reorganization after transposition is quite different from the outset. The superiority of the higher forms may be due in large measure to the greater differential control of motor coordination which is present at the start and not entirely to greater physiological plasticity of the nervous tissue *per se.*

The few brief reports of the effect of muscle transposition in the face (Jianu, 1909; Brunner, 1926) for treatment of facial paralysis in man are incomplete and add nothing essential to the above general picture.

Transposition of Ocular Muscles

The foregoing cannot be generalized to apply to recovery after the transposition of ocular muscles, which appears to present special features and has a literature of its own.

Experimental

Marina (1912, 1915) transplanted the insertions of ocular muscles in the monkey and reported an immediate restoration of normal coordinated eye movements in both voluntary and automatic reactions three to four days after operation. On the basis of his results, he concluded that the nuclei and association tracts of the central nervous system have no fixed and predetermined function, as is traditionally supposed. Later Dusser de Barenne and de Kleyn (1928) transposed the external and internal rectus muscles in the rabbit and in 4 out of 8 cases observed normal nystagmus movements of the eyeball as soon as the animals opened their eyes after the operation. They found, however, that the retractor bulbi muscle, present in the rabbit and in most mammals except primates, was capable after extirpation of all six ocular muscles of executing by itself normal horizontal and vertical eye movements. Olmsted, Margutti, and Yanagisawa (1936) transposed the superior rectus muscle to take over the function of the external rectus in dogs and cats. They reported a recovery of normal eye movement as early as three to four days after operation in the best cases. The recovery of coordination was interpreted as being due to a rapid learning process, and it was concluded further that the new central associations were subcortical, because ablation of the eye motor area of the cortex did not abolish the readjustment once it had been established. These conclusions have subsequently been discredited, however, by Watrous and Olmsted (1940), who discovered that the retractor bulbi muscle by itself may in the dog as in the rabbit effect recovery of correct eye movements in all directions. Watrous and Olmsted further transplanted the superior oblique muscle to a point near the internal rectus muscle in rabbits, and recorded the isolated reflex contraction of the transposed muscle following decortication approximately three months after the primary operation. The muscle showed no alteration in its normal timing. This test after decortication did not prove that no reeducation whatever had occurred, but the results did show that at least no adjustments became so fixed as to become truly reflex.

Although observations of good motor recovery after transposition of eye muscles in lower mammals have thus been discredited as evidence of central nervous readaptation in view of the compensating function of the retractor bulbi muscle, the early results of Marina cannot be discarded on the same basis, for this muscle is so reduced in the monkey that it alone could not possibly effect normal movements in all directions. Bartels (1920) criticized Marina's interpretation, however, on the ground that the action of the remaining healthy muscles would be sufficient to produce the responses Marina observed. He pointed out that a single muscle, the internal rectus, is capable of carrying out nystagmus responses to both sides. He believed all Marina's results could be explained without assuming any central nervous reorganization. In many hundreds of records of isolated eye muscle contractions, Bartels never observed any but standard reactions characteristic of the normal, and he disclaimed any such dynamic plasticity in the coordination centers as suggested by Marina. Bethe and Fischer (1931) supported Marina, nevertheless, on the basis that the records of isolated eye muscles attached to a lever cannot be compared with natural reactions where vision helps to regulate eye mùscle coordination.

More extensive experiments on the transposition of the extraocular muscles in the rhesus monkey have been carried out recently by Leinfelder and Black (1941, 1942). They found that coordinated eye movements were recovered as early as eight days after transposing the medial and inferior rectus muscles plus the superior and lateral rectus muscles, leaving the two oblique muscles in normal position. The degree and speed of recovery was not appreciably influenced by placing the animals in complete darkness during the recovery period. The eye movements after recovery were not entirely perfect; a hypertropia was present that increased on looking toward the side operated on; there was restriction of lateral movement; inferolateral movement was absent; and continuous movement of the eyes suggested diplopia. Vertical and medial movements were well executed, however, and the functional disturbances as a whole were considered minor compared to what would be anticipated from the anatomical disarrangement.

When the four rectus muscles were transposed as above and in addition the superior oblique muscle was transected in the same operation, there was then no recovery of coordinated movements. All movements under these conditions were such as should result schematically from the changed position of the muscles. Medial movement of the normal eye was accompanied by upward movement of the eye operated on. When the normal eye looked downward, the eye operated on turned medially. After both eyes had been subjected to the same operation, all movements of both eyes were abnormal, in accordance with the positions of the transposed tendons. These animals were kept four months at least, but there was no sign of any readaptation.

Further experiments revealed that if tenotomy of the superior oblique muscle was delayed following the transposition of the four rectus muscles until recovery of coordination was well established, then the coordinated movements would survive section of the superior oblique. When the superior oblique had already been sectioned in an earlier operation, then coordination was recovered after transposition of the four recti in 2 of 3 cases. Coordination was also recovered when the two pairs of rectus muscles were transposed at separate operations, and the superior oblique sectioned at an intermediate date. The authors assumed tentatively that central nervous reorganization was the most probable explanation of the recovery of coordination. They reasoned that recovery must depend upon visual and proprioceptive cues, and since vision had been eliminated by placing the animals in total darkness, they were inclined to emphasize the rôle of proprioceptive impulses originating possibly in Tenon's capsule.

These experiments, largely confirming and extending the early observations of Marina, would appear to constitute the most outstanding evidence yet presented of radical and rapid central nervous reorganization after muscle transposition. In view of their significance, the experiments deserve special consideration, with thorough and very careful check and control, to be certain that no other interpretation is possible. If it be accepted that central nervous readjustment was actually responsible for the recovery of coordinated movement, then the results are perplexing in several respects. First, if the central integrating mechanisms are as thoroughly plastic and readily adaptable as suggested by the majority of recoveries, why, after certain types of operation should schematic derangement of eye movements have appeared and persisted permanently with no correction? Why too should the same anatomical result of an operation or a series of operations have been accompanied by recovery of normal coordination in some cases and by appearance of distinctly abnormal movements in other cases, depending only on the order of the operations? That the answer lies in the differential effect on the proprioceptive system is difficult to harmonize with other data on the role of proprioception in reeducation and development of motor coordinations. Proprioceptive cues appear to play a very small role in reeducation after transposition of limb muscles in man, according to Weiss and Brown (1941). Insofar as proprioceptive reflexes result in immediate and almost reflex regulation of muscle response, the proprioceptive discharges would be expected to enhance the original unmodified action of the transplants rather than to aid in adaptation. According to Scherb (1938), proprioceptive impulses from intact associated muscles do inhibit rather than aid reorganization. It is also surprising that the central adjustments were achieved either very early in the first few days after operation or not at all. There was no history of gradual improvement by practice, from abnormal movements to correct rotations. When distinct discoordination was produced by the operations, it persisted. Also counterindicating any kind of learning process is the fact that recovery was not appreciably affected by keeping the animals in total darkness during the recovery period. As contended by Bethe and Fischer (1931), one would expect vision to play a very significant role in any central readjustment of eye muscle coordinations (see also Scherb, 1928b).

Any alternative interpretations ought therefore to be carefully considered. Surgery of the type involved must have presented opportune conditions for formation of scars and adhesions. The tendinous insertions of the transposed pairs of muscles normally border close together. After the muscles had been crossed on each other and reinserted, there would be ample opportunity for the overlapping and coalescence of the tendons and also for the formation of adhesions and extraneous tendon connections to points near their original insertions. Because tendon regeneration and scar and adhesion formations are all profoundly influenced by mechanical tensions, it may be presumed that incipient movements of the eyeball effected during the healing period by the undamaged muscles would be an important factor in shaping the mechanical connective tissue relations between transposed muscles and eyeball. The interrelationship between mechanical stress and connective tissue formation under such conditions is a self-reinforcing one, such that if a particular type of movement once got started, it would influence further structural development in such a way as to increasingly favor the same to the exclusion of other types of movement. The action of the intact muscles would be expected to predominate over that of the freshly transposed muscles, except when the intact muscles were very strongly overbalanced. Early predominance of the intact muscles would be favored further than otherwise appeared by the action of the intact retractor bulbi or accessory lateral rectus muscle, the existence of which was apparently not taken into account. This extra muscle is described by Bast (1933) as a distinct 7th ocular muscle one-fourth to one-third the size of the lateral rectus, occurring only as a rare variation in man but prominent in most rhesus monkeys. One may justly question whether the necessity for leaving two or more muscles intact during the healing period in order to obtain good recovery was not because of the influence of the sound muscles in shaping the connective tissue architecture rather than their influence on proprioception and central readaptation. At present either possibility appears equally plausible. Certainly a very careful dissection of the muscles before sacrifice and a detailed check of the exact mechanical action of each muscle and its parts in reflex responses and in reactions to direct electrical stimulation is needed for an interpretation of the results. The authors themselves were judiciously sparing in interpretation and reluctant to draw any final conclusions. Until anatomical checks and further control experiments are available, it seems advisable to adopt a conservative attitude with regard to the existence of central nervous readaptation in these experiments.

Clinical

According to Bartels (1920), beneficial effects of transposing single eye muscles in man can be accounted for entirely on the basis of passive mechanical effects and other factors such as normal synergic action without assuming any central readjustment of the muscle's activation. Jackson (1923) mentions that the common transposition of slips of two neighboring muscles from either side to compensate for a paralyzed muscle requires no central adaptation because these are synergic substitutions.

The superior rectus muscle of the eye is sometimes transposed to replace the paralyzed levator muscle of the lid. The upper lid and eye are naturally raised and lowered together in most activity so that no recoordination is required. Attempts to close the eye forcibly after such operations, however, often are attended by a sudden jerking up of the upper lid. This is said to be corrected usually after a few months. Whether readjustment in this instance involves the gradual dissociation and inhibition of the action of the transplant specifically in a particular movement, or whether it involves merely learning to use a different type of movement altogether that from the beginning did not include action of the transplant, is not clear. In sleep the eye rolls up and the lid comes down. Inability to keep the lid closed during sleep, after substitution of the levator by the superior rectus, is not observed, however (Jackson, 1923), and this has suggested to some that adjustment of coordination is involved. But if the position of the eye in sleep is one of muscular relaxation, as commonly stated, there would be no necessity for readjustment.

EFFECTS OF INTERCHANGING SENSORY NERVES

Distortion of sensory as well as of motor innervation follows the reunion or cross union and regeneration of nerves. Because of the greater numbers of sensory fibers in most spinal nerves and because of the greater heterogeneity of function among sensory fibers, misdirection and abnormal termination probably occur on a larger scale with sensory than with motor fibers. In order that the sensations and responses to stimulation of misdirected sensory fibers may be made adaptive, the central nervous associations must be readjusted in accordance with the new peripheral connections. How the required functional readjustments compare essentially with those required after efferent disarrangement cannot be said without more knowledge of the neural basis of readjustment and learning processes in general. The problem of readaptation on the afferent side has thus far received comparatively little attention in either the clinical or experimental studies.

Results in animals

In a number of cases those who have accepted the reports of recovery of normal motor coordination after experimental crossing of mixed nerves have inferred without more direct evidence that central readaptation to abnormal sensory, particularly proprioceptive, reinnervation must also have occurred along with the motor adjustment. In several instances (Kennedy, 1901, 1914a; Barron, 1934; Anokhin, 1935a), the impulses transmitted over the abnormally distributed sensory fibers have been thought to play an important role in the readjustment process. Since, as explained above, recovery of normal motor coordination is in itself very questionable in such cases, the corollary inferences concerning sensory recovery may be disregarded.

Bethe (1905; Bethe and Fischer, 1931) noticed, after crossing the sciatic nerves from the left to the right hind leg in the dog, that although there was no sign of motor discoordination after regeneration, there did appear definite evidence of false localization of sensation. When the right foot was stimulated, the animal raised the left leg and turned to the left side. These erroneous reactions persisted without correction until the animal was sacrificed, more than a year later. Bethe considered the absence of adjustment in this case an outstanding exception to the general rule, however, and expressed the opinion that correction might have occurred if longer time had been allowed.

The posterior tibial branch of the sciatic nerve was crossed into the ipsilateral forelimb in the rat by Barron (1934). After regeneration the animals responded to stimulation of the forelimb by withdrawing the hind limb as well as the forelimb. Contrary to the results observed by Bethe in the dog, these abnormal responses in the rat were soon completely corrected, until stimulation of the area of the redistributed nerves resulted only in normal responses of the limb stimulated. The functional correction was maintained even in reflex responses to violent stimulation. This constitutes another instance in which it has been inferred that processes at the reflex level have been adaptively reorganized by learning. Similar results were described by Barron after the median and ulnar nerves of the forelimb had been crossed to the distal end of the femoral or sciatic nerves of the hind limb. He deduced that not only was function of the abnormally connected afferent fibers corrected in itself, but in addition that these fibers had played an important role in the correction of the motor discoordination resulting directly from the crossing of the efferent fibers. It was concluded that abnormal associated movements can be avoided after nerve crossing by using nerves with a sufficient number of sensory fibers to be misrouted along with the crossed motor fibers. As already mentioned in citing the motor aspects of these experiments, one can only point out that they are irreconcilable with other observations. The results of crossing sensory fibers observed by Bethe in the dog and more recently by Sperry (1943a) in the rat (see below) are in direct contradiction to these conclusions.

Anokhin and his co-workers (1935a; Anokhin and Iwanow, 1936a) carried out a long series of experiments on the dog in which they crossed the central end of the divided vagus to the peripheral end of various other nerves including the radial median, and subscapular nerves of the forelimb the optic nerve, the lingual nerve of the tongue, and the motor and sensory roots of the 6th and 7th cervical nerves. The experiments were undertaken for the purpose of studying central nervous reintegration, how it occurs, and over how long a period. Upon completion of regeneration after these crosses, abnormal reactions could be elicited from the various regions reinnervated by the vagus. These were most striking and most thoroughly studied after the vagus to radial nerve crosses. Scratching the skin of the shoulder region after regeneration in such cases caused coughing and a guttural rattle. Manipulation of the shoulder muscles caused profuse salivation and vomiting. When the dogs moved about, stimuli from their own activity caused coughing which stopped only when the animals came to rest. Pricking the skin with a pin, and heat or chemical irritation evoked only pain responses. The coughing and guttural rattle reactions were found to be mediated by the fibers of the recurrent laryngeal nerve which were included in the vagus. When these fibers were excluded, the dogs did not cough but still displayed deep anti-peristalsis reactions.

After some months the abnormal reactions began to disappear gradually, until by the sixth to ninth month after operation, strong and continued irritation of the same skin regions on the shoulder produced no abnormal reactions, but only appropriate responses, as after stimulation of normal skin areas. After disappearance of the coughing and vomiting responses, however, prolonged electrical stimulation under light anesthesia of the exposed vagus nerve or the production of an open wound in the skin by a second degree burn lowered the threshold of the abnormal responses so that they reappeared. Slight irritation around the edge of the open wound, for example, would again elicit coughing and vomiting after these could no longer be evoked by the usual means.

The results were taken to demonstrate that the central phylogenetic connections of the vagus nucleus are not at all fixed, but are capable of extensive rearrangement to suit new peripheral connections. The role of the periphery in regulating readaptation of the central associations was emphasized.

That the animals, after disappearance of the abnormal reactions, were able to feel and to localize correctly stimuli applied to the shoulder area of the crossed vagus was to be expected, in view of the extensive overlap in the distribution of cutaneous sensory nerves (Pollock, 1920b; Gutmann and Guttmann, 1942), involvement of subcutaneous and deep sensibility with the stimuli used, and the natural circumferential shrinkage of areas of sensory loss through changes in the neighboring intact nerves (Pollock, 1920b; Weddell, Guttmann, and Gutmann, 1941). It has been reported that due to peripheral anastomoses of nerve branches in the forelimb of the dog, the excision of a single nerve trunk is not attended by a loss of sensation (Gunn, 1886). The conclusion, therefore, that the vagus nucleus had taken on new somatic functions suited to its new peripheral connections in the experiments of Anokhin cannot be accepted in the absence of convincing evidence that the recovered "adequate" responses were not mediated by intact afferent fibers instead of by the crossed vagal fibers.

On the other hand, the gradual disappearance of the incorrect responses seems unequivocal. That the dogs gradually became conditioned so that these stimuli no longer caused coughing and vomiting is not so extraordinary. The type of reorganization involved would presumably be little different from that involved if the animals were repeatedly exposed to natural stimuli conducive to coughing and vomiting, until gradually they became adapted to such conditions. The learning by human patients to swallow stomach tubes without retching and to inhibit overt coughing in certain pulmonary diseases is analogous. Mere inhibition or dropping out of the original reactions after the crossing of sensory nerves does not involve nearly so extensive a reorganization as does the positive reestablishment of appropriate reactions. Gradual adaptive elimination of a direct autonomic reflex like vomiting, however, is nevertheless of some interest in as low a mammalian form as the dog. That the gradual rise in threshold of the abnormal responses may have been due to depressant metabolic or other local effects of the abnormal nerve terminations rather than to a true learning process is an alternative possibility not excluded.

The nerves of one hind foot were crossed into the contralateral hind foot in the rat by Sperry (1942b, 1943a). All the main nerves of the left foot were crossed to the corresponding nerves of the right foot and the remaining small uncrossed nerve branches to the right foot were excised, so that after regeneration all structures below the ankle on the right side were supplied by nerves that had originally innervated the left foot. The primary operation was performed on young animals only 14 to 26 days of age. After nerve regeneration the animals responded to stimulation of the right foot as if it were the left foot that had been stimulated. This was true even in cases in which the left foot had previously been amputated. There was nothing in the rats' behavior to indicate that they were in any way aware of the illusory nature of these abnormally referred sensations. Painful stimulation of the sole of the right foot caused the animals to withdraw the left leg instead of the right, at the same time to shift the entire weight of the hind quarters onto the right leg, and further to extend the right leg directly against the offending stimulus. These extremely maladaptive reactions, instead of being rapidly corrected after their initial appearance, became more exaggerated as regeneration became complete and thereafter persisted without adjustment as long as the animals were kept, ten and one-half months after operation. Attempts to train the rats by various means to correct the reversed hind limb reflexes were in vain. At the end of ten and one-half months sores in the right foot or painful wire clips pinched into the sole of the right foot caused the animals to walk about on three legs, holding the uninjured left leg in the air and consequently also placing extra pressure on the source of the pain in the right foot.

In contrast to the absence of readjustment of direct reflex responses, the animals did show evidence of learning to locate and remove wire clips pinched on the skin in the area supplied by the redistributed nerves. This apparently did not involve a complete adjustment to the degree that the clips actually felt as if they were on the right foot, for the animals continued commonly to make false turns to the left side and to lick the wrong foot. Nor did this type of learning affect the erroneous reflex withdrawal responses. Even in the act of pulling the clips out of the correct foot, the wrong foot continued to be withdrawn reflexly, and frequently the extra irritation caused by pulling at the clips made the rats abandon the clip on the right foot in order to wheel around and lick the left foot. This persistence of original reflex patterns after adjustment had been made in closely associated activities of a more voluntary nature demonstrates a distinct difference in the susceptibility to reeducative adjustment of different types of central integration patterns. The automatic spinal reactions to strong pain remained quite refractory to readaptation in contrast to the deliberate cortically mediated localizing responses.

Recently Obrador (1942a) tested sensory recovery, as indicated by placing and hopping reactions in cats and dogs, after crossing the peroneal and tibial nerves. These reactions were found to be absent or very defective. Pain sensitivity was roughly recovered, but there was no attempt to test differential function of pain fibers in different parts of the reinnervated areas.

Results in man

Human subjects offer a great advantage for studies of sensory recovery following nerve regeneration, in that they can give direct information regarding their subjective sensory impressions. One would expect the extreme displacement of sensory fibers which must have followed any success with lateral implantation of one nerve into another, as practised in the older clinical nerve surgery, to have resulted in conspicuous distortions of cutaneous localization and other sensory functions. The reports of such partial nerve crosses in man, however, apparently contain no mention of pertinent points on the quality of recovered sensation. Relevant observations of functional recovery after sensory fiber interchange in man are scarce and seem to be based entirely on recoveries following straight reunion of the ends of the same nerve.

General sensory disturbances, such as one would expect to result from chaotic misarrangement of the innervation pattern, have been recorded in some of the more critical examinations of recovery after regeneration of limb nerves in man. Sensory defects in the hand after regeneration of the median and ulnar nerves have attracted particular attention (Sargent, 1920; Stopford, 1930; Ford and

Woodhall, 1938; and others). After regeneration of the ulnar and median nerves, sensations from the affected parts of the hand tend to be diffuse and indistinct. The hand is found to be of slight practical service, even though all the muscles have recovered their volume and contractility. Patients find they lose grip on their tools, the hand fails to function satisfactorily when it is not watched, and is almost useless in the dark or in conditions where it cannot be seen. Generalized pain, tactile, and thermal sensibilities may show good restoration without any corresponding improvement in the refined discriminatory sensory functions. Absent or faulty sense of passive movements of the fingers, uncertainty as to which finger has been touched, gross impairment of two-point discrimination and of stereognosis, and erroneous reports of the mode of stimuli have all been described in cases in which the recovery was said to have been good in a quantitative sense. Head (1920), after prolonged and thorough examination of the affected cutaneous area in his classical experiment, was still making gross errors in the compass test five years after nerve section. The general level of sensory recovery described by Head is rarely approached in clinical cases, according to Stopford (1926), even after primary nerve suture under ideal conditions. Lanier, Carney, and Wilson (1935) stated that the reinnervated cutaneous regions in their experiments never recovered normal sensitivity from the point of view of the character of the effects of areal stimulation. Dallenbach (1931) found it impossible to compute a two-point limen in a reinnervated cutaneous area because of the abnormal disorderly state of the recovered sensibility. Persistence of such general defects as the above for at least three to five years after nerve suture has been recorded in a number of cases, and Ford and Woodhall(1938) doubt that it is possible ever to correct them by reeducation.

More refined analysis of the effects of nerve shunting on recovery of cutaneous sensation is possible in man through the testing of individual sensory "spots." Such tests have been carried out most thoroughly after deliberate experimental section of cutaneous nerves in human subjects. The great diversity in the functional properties of the different sensory fiber types of any large limb nerve makes possible schematically a host of abnormal nerve-end-organ recombinations, following the random redistribution of fibers in regeneration. Two general classes have been recognized by Stopford (1930): (1) Termination of fibers in atypical tissues or end-organs, as when fibers of the articular surface of a joint become misdirected to tactile endings in the skin. Terminations of this first type lead to erroneous impressions of the mode or quality of stimulation. In the given example, tactile stimulation may elicit a sensation not of touch but of movement of a joint. (2) Termination of fibers in the correct type of tissue or end-organ but in a foreign area of the body, as when cutaneous tactile fibers of one finger become misdirected to cutaneous touch endings in a different finger. Tactile stimulation of the reinnervated finger is then perceived as touch but is localized incorrectly to the finger in which the fibers originally terminated. Terminations of this type lead directly to false localization and defects of stereognosis and other functions involving spatial relations. The distinction between these two classes of abnormal sensory termination is of some aid in approaching the problem of recovery, but actually the different possible anatomical recombinations and resulting types of functional confusion are manifold. Lack of knowledge regarding the normal mechanisms and anatomical requirements of sensation, and also regarding the extent to which different fiber types are able to make functional termination in foreign tissues and end-organs, further prevents detailed formulation of the readjustment problem.

Errors of the first type mentioned above, i.e., of the quality or mode of sensations elicited from cutaneous points, have actually been reported in only a few instances. Stopford (1926, 1930) found that pressure stimuli sometimes evoked sensations of burning or of movement at a joint. He suggested that the growth of heat, pain, and posture fibers to tactile end-organs or of pain fibers into heat, cold, or localization pathways would account for these and other odd responses he had observed. Ford and Woodhall (1938) also reported errors of similar nature. In both accounts it has been considered unlikely that this type of functional abnormality could be corrected by reeducation. Whether the failure of most other investigators to notice modal errors of this kind should be attributed to an actual scarcity of the phenomenon, or to the fact that it has not been adequately searched for, remains to be determined.

A persistent generalized intensification of all modes of sensation is apparently conspicuous in reinnervated areas and has been widely reported. There has been little agreement as to its cause

(Trotter and Davies, 1909, 1913; Boring, 1916; Head, 1920; Stopford, 1930; Lanier, Carney and Wilson, 1935), however, and none of the authors have directly ascribed this intensification to fiber misdirection.

The second type of error mentioned above, namely, erroneous localization or false reference of sensations, has been reported commonly in nearly all detailed descriptions of the recovery of cutaneous sensibility after nerve section and regeneration. Sensations of touch, temperature, and pain have been found to be misreferred consistently to various distant points within the region supplied by the regenerating nerve. The sensations are most commonly referred to more distal points, but in the later stages of regeneration reference to proximal and transverse points also occurs. Correctly localized sensations may be present from the start, along with the falsely referred sensations, or may appear in the later stages. A single point stimulus may be referred to two or even three distant points, and Trotter and Davies mention curious instances in which stimuli were localized at the point of nerve section proximal to and outside the cutaneous area supplied by the severed nerve. Stopford, however, said misreference is always to points within the affected area. Trotter and Davies, who apparently paid more attention to the phenomenon of false reference than others, reported that it was one of the earliest and most characteristic accompaniments of recovery and also one of the most persistent. They stated that in some of their cases it remained years after the reinnervated areas had recovered approximately normal sensory acuity. Head, Stopford and others, however, have emphasized that reference disappears with the return of epicritic sensibility. Despite these inconsistencies, all seem to agree that false localization at least tends to give way to correct localization.

The cause of false localization and the reason for its disappearance remain controversial. Langley (1908) and Osborne (1909) believed it was produced by shunting and abnormal termination of afferent fibers, and that its later disappearance was due to readjustment and reeducation of the nerve centers. This view was particularly championed by Stopford (1926) and has since been widely accepted (Lee, 1929; Lanier, Carney, and Wilson, 1935). Boring (1916) accounted for misreference in terms of multiple innervation and the action of inhibitory and secondary fibers. He too believed it disappeared with practice. Head, however, considered misdirection of fibers inadequate as an explanation. Although Trotter and Davies did not contest Langley's hypothesis that misreference is due to misconnections, they, like Head, felt there was more to it. They attributed it primarily to stimulation along their course of newly regenerated hypersensitive fibers, the sensations being referred to the point of the fibers' termination. Gradual return of correct and disappearance of referred sensations they attributed to the formation of end-organ connections and consequent maturation of the fibers. Schafer (1927, 1928) likewise attributed misreference to excitation of fibers along their course instead of at their end-organs. Hoffman (1915) cited cases where peripheral reference of sensations seemed clearly to be caused by stimulation of the outgrowing fibers at their tips or along their course far proximal to any terminations.

That all false reference in the above studies has been due to stimulation of fibers along their course, however, is difficult to reconcile with other facts. Stopford argues, for example, that false localization does not appear in nerve regeneration when a nerve is merely crushed and not severed. Also it has been observed that touch, pain, cold, and warmth all show these abnormal references, and that they are elicited selectively by the correct mode of stimulation. Trotter and Davies therefore inferred that the nerve fibers themselves are selectively sensitive to different modes of stimulation, but Stopford, Schafer, and others have rejected this. Long persistence of false reference when it occurred was attributed by Trotter and Davies to the presence of excess fibers which had not formed end-organ connections and had therefore remained uninsulated and hyperirritable, but as already mentioned, others have denied that false localization persists beyond the first stages of recovery. Trotter and Davies mention that rubbing a point to which itching pain is falsely referred may give considerable relief, even though this point be more than a foot from the stimulated spot. Stopford assumed localization to be mediated by a special set of localization fibers, but others assert that localization is mediated by the regular pain, touch, and temperature fibers (Lanier, Carney and Wilson, 1935). A thorough comparison of the effects of nerve regeneration without shunting, as after crushing or fixing with alcohol, and of regeneration with extensive shunting, as after complete severance, would be extremely helpful on a number of these problems. In Schafer's study on this plan pertinent points were not recorded, and in the work of Lanier, Carney and Wilson the surgical method of injecting the anesthetic and alcohol into the nerves leaves it uncertain as to whether there may not have been considerable shunting of fibers.

Disregarding the numerous contradictions of the various reported facts and opinions, one gets the general impression that less distortion of sensory mode and localization have been found in these studies than would be predicted schematically on the supposition that the sensory fiber regeneration and termination is random and nonselective. If localization depends upon stimulation of at least two fibers, as inferred by Weddell (1941c), then it is indeed surprising that any sharp localization, correct or false, was recovered at all, since the chances of both members of the correct pairs of fibers terminating together in the same sensory spots would be exceedingly slight on a purely fortuitous basis. Nevertheless, the abnormally referred sensations have been reported as being very distinctly localized with precision at the referred point. This precise but erroneous localization of sensations could hardly be ascribed to learning. In addition, the falsely referred sensations were often accompanied by correctly localized "local" sensations. To what extent these correctly localized sensations in these older experiments were attributable to the overlap of neighboring fibers of cutaneous and deep sensibility is debatable.

Further discussion, in an attempt to arrive at some conclusion from the observations thus far available, is useless. The investigators have disagreed upon too many issues. At the time the studies were made little was known of the anatomy of cutaneous innervation, particularly with regard to nerve overlap and multiple innervation of sensory spots. The complications arising from hypersensitivity in the intermediate zone, and from the sprouting and invasion of collateral fibers (Gutmann and Guttmann, 1942) were not clearly recognized. The experimental approaches have been guided largely by the original ideas and observations of Head, while problems such as those created by nerve fiber shunting have remained unrecognized or at best have received only casual attention. Some critical deductions might be gleaned from these older studies if knowledge of the anatomy and physiology of normal cutaneous sensibility were available as a basis for judgment, but as yet there is still little agreement about even the most fundamental aspects of normal cutaneous sensation (Nafe, 1934; Lewis, 1937; Stone and Jenkins, 1940; Rothman, 1941; Gilmer, 1942a, b; Walshe, 1942; Livingston, 1943). In summary, it is impossible to say from the reports to date whether or not any reeducative central nervous adjustments are involved in the partial recoveries of sensitivity that follow cutaneous nerve regeneration. With the increased knowledge of the distribution and physiology of sensory fibers (see Weddell, 1941b; Tower, 1943; Bishop, 1944, among others) and with the numerous advances in methods for study of the sensory mechanisms, many of these points of confusion left by the older studies might soon be resolved.

TRANSPOSITION OF SENSE ORGANS

The transplantation or grafting of pieces of skin sometimes results in abnormal cutaneous sensation and presents a problem of central nervous readaptation. Generally where a piece of skin is transplanted with most or all of its nerve supply severed, localization within the transplanted area, according to Purdy (1934), is restored correctly by the ingrowth from the surroundings of those fibers which originally supplied the area. One might expect, however, that although localization would be grossly correct under these conditions, discrimination of spatial relations within the graft area itself, and also of the mode of stimulation of individual sensory spots, might be abnormal. Although some observations of recovery of sensation in free skin grafts have been reported (Kredel and Evans, 1933; Davis and Kitlowski, 1934), a thorough, detailed study with the problems of nerve regeneration and the reestablishment of appropriate end-organ relations in mind is still needed and might throw considerable light not only on questions of recovery but also on some of the points of confusion regarding normal sensory function.

When a flap of skin is shifted to a new position with most of its innervation intact, sensations elicited from the transplant are the same as before transplantation, i.e., adapted to the old position instead of the new. For example, Douglas and Lanier (1934) report the results of transposing a flap of skin from the upper to the lower lip, with one end of the flap remaining intact at the corner of the mouth. Stimuli applied to the lower lip were thereafter referred to the upper lip. Such transposition of skin flaps is somewhat analogous on the sensory side to muscle transposition on the motor side. In both situations there is retention of the original systematic innervation of the transposed part, so that neural interrelations are not thoroughly disrupted at the neuron level as after nerve regeneration. The problem of readjustment is therefore quite different, being presumably much simpler than when the function of individual sensory spots, even of individual sensory fibers, must be corrected and resynthesized into an orderly system. Douglas and Lanier reported that their patient, cited above, gradually learned to localize correctly stimuli applied to the transposed skin on the lower lip. They concluded therefrom that localization depends mainly on habit formation.

Contradictory results were reported by Purdy. He studied localization in a flap of skin from the volar surface of the terminal phalanx of the middle finger which, after accidental amputation of the end of the finger, had been folded over the cut end and sutured to the skin of the dorsal surface with about 6 mm. folded over beyond the end of the finger. The patient was thirteen years old when the transposition was made. Ten years later, stimuli applied to the flap on the dorsal surface were still invariably localized in an illusory fashion to the volar side of the non-existent first phalanx. A single touch at the suture line felt double, one dorsal and the other ventral, with the finger in between, even though the patient was looking at the stimulus. The reports of both Purdy and of Douglas and Lanier fail to distinguish clearly between the patient's immediate subjective impression and his ability to interpret this so as to localize accurately. In Purdy's case it seems clear that the patient could have localized these stimuli correctly by word or gesture despite the illusory subjective impression—obviously so, when he was allowed to watch application of the stimulus. From Douglas and Lanier's report, however, it was not clear whether the stimuli came actually to be felt in the lower lip or whether the patient had simply learned that stimuli which felt to be at one place were really at another. No controls were given that would indicate in any way what actually had been learned by this patient. Also the gradual invasion of fibers from the lower lip into the partially denervated graft was a complicating factor in this case.

The readjustment in the report of Douglas and Lanier was compared to that achieved by Stratton (1896, 1897) after wearing lenses which inverted the appearance of the visual field. Stratton reported that eventually the inverted visual field no longer appeared upside down under certain conditions of relaxed attention, and his results were interpreted by himself and many others as indicating that complete adaptation to visual inversion would occur with prolonged practice. This has been contradicted, however, by the more extensive experiments of Ewert (1930, 1936, 1937), in which 3 subjects wore the inverting lenses more than twice as long as did Stratton, and also by the unpublished study of Peterson (Ewert, 1936), who wore Ewert's apparatus about three times as long as Stratton and who took care to repeat Stratton's procedures. The visual field in all these subjects continued to appear upside down without noticeable change. Directions were seen reversed in movement, and this illusion was so strong it could not be inhibited. Distances tended to appear inverted, and judgment of distance remained poor. A complete adaptation to this sensory inversion with prolonged practice was considered by Ewert to be highly improbable. Nevertheless, certain types of overt localizing reactions and compensatory motor adjustments to the sensory reversal were readily established. These motor adaptations were characterized by typical learning curves.

Comparable visual disorientation effects produced surgically in amphibians have been found to persist indefinitely without correction even of deliberate overt motor reactions (Sperry, 1943b–1945). When the eyeball of an amphibian is rotated on its optic axis through 180 degrees, the animal's behavior thereafter indicates that the visual field is seen upside-down and reversed about the optic axis. Objects above the head are falsely localized to a position below the head, objects in front are localized to the rear, etc. Perception of the direction of movement across the visual field is reversed, as illustrated by optokinetic and pursuit reactions. Persistent circus movements also result. When the eye is transplanted to the contralateral orbit with either the nasotemporal axis or the dorsoventral axis inverted, and the perpendicular axis at the same time normally oriented, then vision after nerve regeneration is correspondingly reversed with respect to the inverted axis of the eye, but normal with respect to the axis correctly oriented. For example, if the dorsoventral axis of the eyeball is inverted, objects in front and above the animal are localized in front and below, whereas if the nasotemporal axis is inverted, objects in the same position are localized above and to the rear. Also in the latter case horizontal optokinetic reactions are reversed, and continual circus movements are exhibited. When the optic nerves are crossed with each other, then vision after recovery is contralaterally reversed in mirror-image fashion. Objects on the right side of the animal are misreferred to corresponding positions on the left side and vice versa, as indicated by escape, feeding, and optokinetic responses. Perception of the direction of movement in the visual field around the dorsoventral body axis and also around the longitudinal body axis is reversed, as indicated by reversed optokinetic reactions and pronounced circus and swaying movements of the head on these two axes. These maladaptive distortions of visuomotor coordination, diagrammatically correlated with the anatomical sensory recombinations, are apparently not subject in the amphibians to any appreciable correction by central nervous reorganization.

P. T. Young (1928) found that a right-left reversal of auditory localization produced in man by pseudophones persisted without correction after the pseudophones had been worn for 58 hours over a period of 18 consecutive days. Some compensatory adjustments to the auditory reversal were made by increasing dominance of vision over audition and by deliberately turning in the opposite direction from which sounds seemed to come. This, like the results of lenticular inversion of the visual field, is another example of persistence of illusory sensations in man with attendant correction of associated overt responses by learning.

The "phantoms" which appear after various types of amputation have been compared to illusory sensations resulting from nerve redistribution and skin grafting. Phantom limbs sometimes fade out completely in the course of years, but they may also persist permanently without change (Gallinek, 1939; Riddoch, 1941). It is questionable whether much positive central nervous reorganization is involved in the fading of phantom limbs. The process may be entirely inhibitory, rather than reconstructive, and the inhibition may be active or simply a passive dropping out of excitations in the centers involved. Persistent phantoms are usually associated with intractable pain, which apparently prevents fading by keeping the limb centers in a state of high excitability. It may be argued that the failure of the spatial attributes of the sensations to become adapted to the new body form under these conditions is demonstration of a certain lack of plasticity and adaptability in the central associations concerned, but final judgments in this regard had better be postponed until the underlying causes of such phantoms are more thoroughly understood.

The results of skin transplantation, auditory reversal with pseudophones, and lenticular inversion of the visual field in man indicate that motor responses can be readjusted in some degree to suit this kind of sensory alteration, but the problem of reeducation under such conditions is simpler than and must be distinguished from that following random reconnection of individual sensory fibers. To what extent the adjusted responses may eventually become as rapid and automatic as normal reactions remains to be determined. Nor is it clear whether the subjective sensations themselves can ever be corrected by reeducation. The little evidence available indicates not.

SUMMARY AND DISCUSSION

Since the time of Flourens the weight of authority has favored the view that complete or nearly complete functional adaptation after disarrangement of nerves and end organs may be brought about by reintegration of the central nervous relations of the motor or sensory nerves involved. Critical consideration of the evidence, however, reveals little that supports even the more moderate assertions of the past concerning central nervous reintegration. Most of the more remarkable functional recoveries that have been recorded appear to have been cases in which various types of compensatory adjustment on the part of the intact system, along with local mechanical and trophic changes in the affected parts, have together produced a serviceable effect which has been erroneously interpreted to be the product of extreme revision in the central synaptic associations of the affected peripheral nerves. Many factors which may contribute to such spurious recoveries, both motor and sensory, have been cited in the text. Past failure to analyze carefully the various underlying factors contributing to readaptation, and especially failure to distinguish between the indirect compensatory type of adjustment and adjustment in which the function of the affected nerves and end organs themselves is directly involved, has rendered invalid a large percentage of the older conclusions regarding the reintegrative capacities of the nerve centers.

When those observations and experiments in which spurious recovery has not been controlled are ruled out, the capacity of the mammalian nervous system to readapt the function of its disarranged nerves and end organs appears quite limited.

Immediate Spontaneous Reintegration

There remains no convincing support for the idea of recovery by instantaneous dynamic reorganization as postulated by Marina (1912, 1915), Bethe and Fischer (1931), Manigk (1934), and Goldstein (1939). These authors, among others, have asserted that new adequate central coordination patterns emerge immediately in direct response to new peripheral arrangements, without any practice or learning being necessary. Control of central nervous coordination is presumed accordingly to be mainly peripheral and to depend upon some kind of dynamic organization which is relatively independent of structural pattern and which automatically achieves adaptive functional effects. As it stands, the evidence definitely contradicts the supposition that any readaptation is achieved by spontaneous dynamic readjustment in this sense. There has been no convincing positive record of this type of recovery, whereas there are a large number of opposing accounts in which either dysfunction has persisted without any readjustment or else some adjustment has occurred but has clearly required time and practice. Functional readjustment, insofar as it has been conclusively demonstrated and especially where comparisons between man and other species are possible, appears to parallel a limited learning capacity rather than an all-pervasive plasticity intrinsic to the organization of central gray matter *per se*. It cannot be denied that some comparatively rapid adaptations may conceivably occur under particular circumstances, as after certain very favorable muscle transpositions, but the amount of central reorganization involved is relatively negligible, and the implications for the nature of central nervous organization are certainly far from the type of thing originally supposed. For practical purposes it would seem best, on the basis of the evidence now available, to relinquish altogether any hope that immediate spontaneous reorganization will effect correction of function after nerve misdirection or muscle transposition.

Local Morphological and Physiological Readaptation Phenomena

Before considering the possibilities of readjustment by the ordinary learning process, mention must be made of certain other factors essentially non-functional in character which also may contribute to readaptation, particularly after nerve regeneration. These include various growth-regulating, trophic, and other local physiological and biochemical phenomena which there has not been occasion to present in any detail in reviewing the literature. As a whole these phenomena have received little study, and little is yet known about them. Their possible significance nevertheless deserves attention. In restoration of function their effects may easily be confused with those of learning, and hence it is quite important to distinguish between recoveries due to reeducation and those due to factors such as are mentioned below.

Owing to various qualitative influences tending to prevent adverse nerve fiber terminations, to cancel the function of adverse terminations, and even to foster in a positive manner the formation and function of appropriate over inappropriate terminations, the functional results of nerve regeneration may be less maladaptive than would be anticipated from the extent of fiber shunting in the scar region. According to Elsberg (1917), for example, original motor fibers tend to succeed over foreign axons when both are given equal opportunity to reinnervate a skeletal muscle. A similar selectivity may also be exercised in the termination of the different sensory fiber types in the skin and elsewhere. According to Dale (1935), adrenergic fibers are unable to establish transmissive connections with cholinergic endings, and vice versa. Langley (1898a, 1900) reported that regenerating preganglionic fibers of the sympathetic trunk form connections discriminately in the ganglia with their own particular class of post-ganglionic neurons. There is suggestive evidence that in amphibians nerve regeneration results in a selective systematic reestablishment of original synaptic associations in the centers (Sperry, 1943c–1945). Qualitative relations between regenerating peripheral nerve fibers and end-organs may be influential in determining which of the many extra fibers that reach the periphery are to survive and attain maturity (see Young, 1942). Thus, although nerve fibers clearly can be forced by nerve crossing to form, and do regularly form after straight nerve reunion, extensive abnormal connections, it cannot be concluded that there are no factors whatever tending to favor formation of appropriate over inappropriate terminations. Any such selectivity of regeneration and termination must depend apparently upon contact effects entirely (Weiss, 1941b).

A selective readaptation of nerve fiber connections may continue to occur after regeneration is in the main completed. For example, if the regenerated nerve terminals in the skin remain in a state of flux, degenerating and regenerating anew (see Speidel, 1942; Weddell and Glees, 1942), selective affinities favoring the perpetuation of appropriate over inappropriate relationships might gradually make the former increasingly predominant, effecting a slow sensory improvement difficult to distinguish from improvement by learning. We still do not know whether the regeneration and development of new sensory end-organs is conditioned in any way by the character of the different fiber types with which they become connected, although some approaches to that problem have been made (Dijkstra, 1933). Misdirection of salivary fibers in the region of the facial nerve leads to excessive lacrimation but not to synchronous contortions of the facial muscles. Also misdirection of the motor fibers of the facial muscles leads to mass movements but not to synchronous lacrimation and salivation. These selective effects might be due to discriminate fiber termination or to differential chronaxies. The functional effects of the regeneration of sensory fibers into motor channels, or vice versa, are commonly said to be cancelled out. Polarity of reflex conduction may be partly responsible. Incidentally, in contradiction to general belief, Ballance (1932) reported that a sensory nerve crossed to the facial could correct the muscle atrophy of facial paralysis and effectively avoid any associated movements. A predilection of outgrowing sensory and motor fibers for sensory or motor end-organs respectively has been demonstrated in development (Hamburger, 1928; A. C. Taylor, 1944). It has been suggested (Weiss, 1936, 1941c) that different skeletal motor fibers in amphibians may be selectively sensitized to respond only to specific central excitatory agents, and that this sensitization may in turn be regulated after nerve regeneration by qualitative relations in the periphery. Results obtained with sensory fibers (Weiss, 1942) have been interpreted on a similar basis. Hypersensitization produced in the nerve centers, ganglia, or periphery by denervation (Cannon and Haimovici, 1939) may result in increased function of the remaining elements, tending to correct the paralysis (see also Spiegel and Démétriades, 1925). Or the denervated parts may stimulate or permit development of collateral innervation from nearby intact fibers and thereby have their function restored (Fort, 1940; Weddell and Glees, 1942; Geohegan and Aidar, 1942; Speidel, 1942).

The foregoing is sufficient to suggest some of the many ways in which anatomical and physiological relations might conceivably be readapted locally so as to limit the abnormality of function after nerve regeneration, and in varying degrees obviate reeducation. Such factors would be of less influence after nerve crossing than after straight nerve reunion. The evidence to date has left obscure the actual extent to which readaptation is assured by such means in man and the mammals. The above heterogeneous examples are intended to be illustrative and suggestive only, and are necessarily speculative in large measure. Because of the lack as yet of positive knowledge of these aspects of recovery, one can only point summarily to the negative evidence that after all such local readaptation processes associated with nerve regeneration have been completed there still remain in mammals, following straight nerve reunion, as well as nerve crossing, extensive abnormalities and deficiencies of function which are dependent for correction upon reeducation.

The situation in the amphibians, however, is quite different, and special mention must be made of the paramount role which factors belonging in the above category play in recovery in this group. In this class of vertebrates it is a growth-regulating type of phenomenon entirely which is responsible for readaptation. Learning plays no part. After disarranging nerve connections to the limb muscles, normal muscular coordination is restored (Weiss, 1941c), and the recovery is much better than anything which occurs in the higher mammals, including man. Also after severance and various disarrangements of the intra-neural fiber pattern of the optic nerve, well organized visual perception is restored (Stone and Zaur, 1940; Sperry, 1943c–1945). Experiments have shown that these orderly and practically complete functional recoveries in the amphibians are definitely not achieved through practice and experience but are systematically predetermined by growth-regulating factors. Apparently the same factors which are responsible in ontogeny for the development of normally adaptive anatomical and physiological neuron relationships between center and periphery remain influential in adult nerve regeneration. This particular type of adaptation is correlated with the lasting embryonic lability of amphibian tissues, and apparently does not occur in the mammalian organism except in early embryonic stages (Weiss, 1935, 1936; Sperry, 1941).

After disarrangements in amphibians which cannot be entirely remedied by such growth-organizing factors and which therefore necessitate reeducative correction, as after reorientation and transplantation of muscles, limbs, and eyes, then a maladaptive effect inevitably ensues which remains uncorrected. For further discussion and analysis of the special mode of recovery in amphibians, see Weiss (1936, 1941c) and Sperry, (1943b–1945).

Recovery by Reeducation, the Learning Process

With intrinsic growth and local physiological processes of readjustment reduced to an indistinct, but what seems to be a comparatively minor, role in man and the mammals, and with spontaneous dynamic reintegration negated by the evidence, there remains what has generally been considered the major source of readaptation, the learning process itself. "Reeducation" of course implies a process of learning which is taken here to include all that is commonly encompassed by the term, from the slowest trial and error forms of learning to the rapid conceptual and insightful types. Correlated with the general lack of any precise knowledge of the neurological basis of reeducation, there has been scarcely any limit to the degree and types of central nervous reintegration which have been attributed to it. The evidence, when reviewed critically in the light of the more recent results, however, suggests that the learning capacity has marked limitations when it comes to correcting the dysfunction of misarranged nerves and end organs. Only particular forms and orders of central nervous reintegration seem to be possible, and these with a wide range of varying difficulty, while others are apparently wholly beyond the scope of the learning capacities even of man. Because of the varying effectiveness of reeducation in correcting different kinds of malfunction, it becomes of practical importance for prognosis and other purposes to try to determine in greater detail the essential neural nature of reeducation, its central locus, and its inherent limitations and potentialities.

Central locus of reeducative adjustments

There have been a number of attempts to determine the locus of reeducation in the nerve centers by cortical stimulation or by lesion methods (see Stefani, 1886; Kennedy, 1901, 1914a; Osborne and Kilvington, 1910a; Maragliano, 1912; Ballance, 1932; Bethe and Fischer, 1931; Olmsted, Margutti, and Yanagisawa, 1936; and others). In nearly all such cases, for reasons already elaborated, it is quite doubtful that the assumed readjustments had actually occurred. The results of cortical stimulation predominantly have been the same as would be expected if no central nervous readjustment had taken place. Those instances, on the other hand, in which central readjustments were indicated either by the results of cortical stimulation or by survival of adjusted behavior after decortication, cord transection, etc., appear to have been cases of spurious recovery not involving adjustment in the function of the affected parts, as supposed. There has as yet been no satisfactory experimental demonstration of the precise location in the central nervous system of the adjustments involved in reeducation.

The frequent casual references in the literature to "reeducation within the facial nucleus," "reintegration in the spinal limb centers," "readaptation of cortico-spinal connections," and the more emphatic assertions of Anokhin, Goldstein, Bethe, Osborne and Kilvington, and the rest that even the most basic phylogenetic reflex associations of the spinal system undergo adaptive reintegration after nerve-muscle rearrangements are all without reliable experimental foundation. The evidence on the whole tends to refute such assumptions and to indicate that reeducative neural adjustments, like those of learning under normal conditions, are confined to higher brain relations and never effect any switching of basic neuron associations of the spinal cord or of the primary sensory and motor nuclei of the brain.

The question may be raised, however, whether the attainment of automaticity by long practice might not result eventually in descent of the central reorganization to lower motor levels. Reliable direct evidence is lacking on this point, but what little is known of the basis of habit automatization in general (Lashley, 1921) suggests that the descent of central reorganization to subcortical levels, if it occurs at all, is not sufficient to make an acquired habit independent of its cortical organization. Weiss and Brown (1941) reported relapses into old motor patterns many years after transplantation of the hamstring muscles in man, indicating that the original basic coordination patterns remain intact under superimposed learned adjustments (see also Weiss and Ruch, 1936). It remains very doubtful that even continued practice effects any remodeling of the basic spinal and brain stem integration patterns.

Neural nature and limitations of reeducation

What little is known of, and further, all that is known *not* to be true of the neural basis of learning under normal conditions (Hilgard and Marquis, 1940) seems to apply to reeducation after peripheral disarrangements. There is no indication that reeducative neural adjustments following nerve regeneration and muscle transposition are any different from those involved in learning under normal circumstances. They would seem not to be any more elementary or simple, nor their location in the brain any more circumscribed than are the still obscure and elusive engrams of ordinary habits of motor skill and sensory discrimination (Lashley, 1931).

The commonly recognized laws and limitations of learning such as pertain, for example, to the transfer of training from one performance to another, to the complexity of performance, frequency of repetition, speed, etc. apply, as far as can be ascertained, equally well to reeducation after nerve-end organ rearrangements. Further discussion, however, is restricted to mention only of certain limitations of the learning process particularly pertinent to the conditions of nerve regeneration and the transposition of muscles and sense organs. It is highly significant from the theoretical viewpoint that the results of experiments on nerve interchange and end organ transposition suggest characteristic and basic limitations of the learning process which were not previously brought out by observations under other conditions, and which may serve as important clues to the essential character of the neural basis of the learning process itself.

On the motor side, the evidence suggests a limit in the minimum size of the functional units which are subject to dissociation and recombination by learning. Corollary to the conclusion that learning depends upon reorganization in the higher centers is the further deduction that reeducative dissociation and reintegration of motor patterns must therefore be restricted by the degree of refinement in the relations between the higher centers and the spinal motor system. One would consequently expect to see an increase in capacity for effecting detailed motor reorganization by reeducation in passing from the lower vertebrates through the mammals to man, correlated with the appearance and increasing elaboration of the cortico-spinal system. A marked increase of this kind is indicated by the data available. The urodele amphibian, for example, does not correct or even inhibit the normal action of the entire limb after transplantation has made the normal limb coordination detrimental to the animal (Weiss, 1937b). In the lower vertebrates it appears to be only generalized movements and orientations of the whole organism that can be recombined by learning. Even the rat is apparently not able to correct or even inhibit separately the movements of one limb joint after muscle and nerve crosses, indicating that the minimum functional units subject to dissociation and recombination by learning are considerably larger in the rat than in man and involve possibly movements of the limb as a whole. In man, not only the action of a single limb joint but even that of individual muscles about a joint can be dissociated and readapted to some extent. The functions of individual motor neurons, however, are not dissociated and reorganized into new adaptive groupings even in man. The minimum functional unit subject to recombination by learning in man seems, therefore, to be approximately the "motor pool" of individual muscles or of the gross subdivisions of muscles with multiple heads. Such minimum recombinable motor elements may vary, however, under different conditions not only between species but also between different parts of the body, exhibiting, for example, greater refinement in the arm than in the leg.

It is important, in view of the foregoing, to distinguish the different orders and degrees of motor readjustment that may be achieved in any single task of readaptation. For example, after nerves have been crossed experimentally to antagonistic muscle groups of the dog's hind limb, varying degrees of improvement over the reversed movements which would otherwise follow, might be effected (1) by simply inhibiting all movement of the affected leg; or (2) by inhibiting movement only of the particular joint involved; or (3) by contracting all the effected muscles as group indiscriminately, to provide a constant rigidity to the joint; or (4) by contracting persistently one of the antagonistic groups alone, to keep the joint fixed in a definite favorable position; or (5) by reversing the timing of one of the antagonistic groups alone, to provide stability of the joint selectively at only the proper phase of leg movement; or (6) by reversing the timing of both groups, to achieve approximately a recovery of correct coordination; or (7), since optimal function would not result with all muscles of each nerve acting as a unit in perfect synchrony, further improvement would be achieved by more refined differentiation and readjustment in the timing and intensity of the individual motor neurons. The central nervous reorganizations involved in these different possible methods of adjustment may vary greatly in their essential nature and in difficulty of achievement. The last and most refined order of reintegration at the neuron level is not required after transposition of muscles, making the task of complete reeducation much easier after muscle transposition than after nerve regeneration. For further discussion of the limitations of reorganization in connection with the functional individuation and hierarchical organization of the nervous system, see Weiss (1941c). Additional limitations and difficulties of motor reorganization correlated with some other types of factors have also been presented above in the section on muscle transposition.

On the sensory side, the possibilities of reeducation vary greatly, according to the nature of the central and motor effects which are produced by the afferent stimuli concerned. Afferent excitations are in part projected to the cerebral cortex but are also short circuited through spinal, cerebellar, thalamic, and other lower levels and may result in any one or all of a variety of different effects, such as the following: (a) immediate overt reflex responses initiated involuntarily before the subject is aware of any sensation; (b) modification and regulation of motor activity without the subject's awareness, as with proprioceptive stimuli; (c) sensations of which the subject is aware and as a consequence of which motor activity is deliberately initiated or altered; (d) sensations which register but which lead to no direct overt response. This list is not intended to be comprehensive (see also Weiss, 1941a) but merely sufficient to serve as a reminder that the central functional associations of different afferent fibers, and even of single fibers, are complex and varied. The problems and possibilities of readapting these central associations are correspondingly varied. In so far as the sensory derangement affects neutral stimuli which lead to no overt reaction, almost any adaptive response could presumably be "conditioned" to the neutral stimuli. On the other extreme, where the stimuli involved evoke spinal reflexes, there arises the problem of readaptation at the spinal level. It is very doubtful that the integrative effects of afferent impulses (Creed, 1931) at the spinal level, or even at cerebellar or other sub-cortical levels, can be directly readjusted in the higher mammals by reeducation. Any improvement must probably come, therefore, in an indirect manner via superimposed activity involving cortical organization. It is still not certain that the central sensory excitation patterns of immediate subjective sensation are subject even to relatively simple corrections in man by any amount of reeducation. Adaptive adjustment of overt voluntary reactions to compensate for certain simple derangements of sensation, on the other hand, has been shown to be not difficult in man, and possible even in the rat.

The task of recovering refined discriminatory sensory functions, following the random regeneration of sensory fibers with consequent disruption of the orderly sensory projection to the cortex, raises special problems which have received little clarification thus far. That errors in mode of sensation owing to the termination of fibers on the wrong class of end organ can ever be corrected by reeducation has been considered unlikely, but there is no actual evidence on the matter. Readaptation of disturbed localization, however, has commonly been assumed to occur. It is quite conceivable that with practice one might learn to localize correctly, under the conditions of random reinnervation, one or a number of individual cutaneous points whose localization was at first misreferred. It seems very doubtful, however, that any amount of practice could restore normal stereognosis and other discriminatory performances involving areal pattern stimulation and necessitating proper adjustment with respect to the relative spatial relations of large patterns of myriad end-organs supplied fortuitously by misdirected fibers. Even the most basic spatial arrangement of cutaneous innervation permitting determination, for example, of whether one point or two is being stimulated, the relative location of two points or of a series of points with respect to each other and the analogous basic organization of proprioceptive innervation upon which pattern perception depends will be completely distorted under such conditions. The task of relearning the basic spatial and proprioceptive values of all the individual misdirected fibers and of all their interrelationships after disarrangement at the neuron level would be one of tremendous complexity. Under normal conditions these basic sensory values are provided automatically through an innate orderliness of associations between the central sensorium and periphery, an innate orderliness which presumably is established in ontogeny by growth processes and not by learning. This interpretation is contradictory to the conclusion of Douglas and Lanier (1934) that sensory "local signs" depend mainly on habit formation; but it is supported by the observations of Purdy (1934), Ewert (1936), Sperry, (1942b–1945), and by other lines of evidence (see especially von Senden, 1932; Hebb, 1937).

Stopford's (1930) contention that "epicritic" cortical sensations are separable from and more subject to reeducation than "protopathic" thalamic sensations is, of course, speculative and based originally upon erroneous interpretations of sensory recovery that have since been abandoned (Walshe, 1942); but too little is yet known to make any final negation or affirmation of the general idea itself. This, along with most of the problems of sensory recovery, only some of which have here been indicated, remains more properly a matter for future investigation than for present speculation or review.

Other things being equal, the degree of differential voluntary control over the functions of the autonomic system tends to be less than over somatic functions, and the evidence indicates a correspondingly greater refractoriness of the autonomic functions to dissociation and reorganization.

It has occasionally been implied or directly suggested, in regard to the substitution or crossing of nerves, that probably (Harris and Low, 1903) the nearer the roots of the two nerves are to one another in respect of the cord segments to which they belong, or (Frazier, 1924) the nearer together the cortical centers presiding over the movements concerned, the easier will be reeducative correction of any incoordination. The choice of nerves for crossing as well as the choice of muscles for transposition would seem in this regard to be primarily a matter of functions subserved, rather than of topographical proximities of nerve roots or motor centers. This is consistent with the conclusion that the reeducative adjustments are not effected in the primary motor or sensory nuclei but involve the higher association centers, and that it is not merely a simple localized switching of anatomical connections which occurs but an operationally organized readjustment of the sort involved in ordinary learning under normal conditions.

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LIST OF LITERATURE

Aird, R. B., and H. C. Naffziger. 1939. Regeneration of nerves after anastomosis of small proximal to larger peripheral nerves. *Arch. Surg.*, 38: 906–916.

Anokhin, P. 1935a. *Reports on the Problem of Centre and Periphery in the Physiology of Nervous Activity.* Gorky State Publishing House, Gorky, USSR.

——. 1935b. Ueber das einheitliche Zusammenwirken des Zentrums und der Peripherie in der Nerventätigkeit. *Sselschenow's Z. Physiol.* (*US SR*), 19: 27–34.

——. 1940. Localization of motor impulses in the central nervous system. *Probl. mot. Nevrol. Psikhiat.*, 8: 15. (See *Psychol. Abstr.*, 1943, 17: no. 1457.)

——, and A. Iwanow. 1936a. Experimentelle Veränderung der phylogenetischen Verbindungen im Gebiet des Nervus vagus. *Pflüg. Arch. ges. Physiol.*, 237: 536–557.

——, and ——. 1936b. Experimentelle Veränderungen der phylogenetischen Beziehungen im Bereiche der spinalen Innervation. *Pflüg. Arch. ges. Physiol.*, 237: 558–570.

Ballance, C. 1923. Some results of nerve anastomosis. *Brit. J. Surg.*, 11: 327–346.

——. 1924. Results obtained in some experiments in which the facial and recurrent laryngeal nerves were anastomosed with other nerves. *Brit. med. J.*, 2: 349–355.

——. 1931. Anastomosis of nerves. *Arch. Neurol. Psychiat.*, 25: 1–28.

——. 1932. A note on the operative treatment of facial palsy. *Brit. med. J.*, 1: 787–788.

——, and A. B. Duel. 1932. The operative treatment of facial palsy. *Arch. Otolaryngol.*, 15: 1–70.

Barron, D. H. 1931. Muscle response to foreign innervation. *Proc. Soc. exp. Biol. Med.*, 29: 184–186.

——. 1932. Muscle response to strange innervation. *Anat. Rec.*, 52 (suppl.): 4.

——. 1934. The results of peripheral anastomoses between the fore and hind limb nerves of albino rats. *J. comp. Neurol.*, 59: 301–323.

Bartels, M. 1920. Aufgaben der vergleichenden Physiologie der Augenbewegungen. *Arch. Ophthal.*, 101: 299–332.

Bast, T. H. 1933. Chap. 18 in *The Anatomy of the Rhesus Monkey*, ed. by Hartman and Strauss. Williams & Wilkins Co., Baltimore.

Bender, M. B. 1936. The nerve supply to the orbicularis muscle and the physiology of movements of the upper eyelid. *Arch. Ophthal., Chicago*, 15: 21–30.

——, and S. Alpert. 1937. Abnormal ocular and pupillary movements following oculomotor paralysis. *Arch. Ophthal., Chicago*, 18: 411–414.

——, and J. F. Fulton. 1938. Functional recovery in ocular muscles of a chimpanzee after section of oculomotor nerve. *J. Neurophysiol.*, 1: 144–151.

Bentley, F. H., and M. Hill. 1940. The possibilities of nerve grafting. *Brit. med. J.*, 2: 352–353.

Berry, C. M., H. Grundfest, and J. C. Hinsey. 1944. The electrical activity of regenerating nerves in the cat. *J. Neurophysiol.*, 7: 103–115.

Bethe, A. 1905. Ueber Nervenverheilung und polare Wachstumerscheinungen am Nerven. *Münch. med. Wschr.*, 1: 1228.

——. 1931. Plastizität und Zentrenlehre. *Hb. norm. pathol. Physiol.*, 15: 1175–1220.

——, and E. Fischer. 1931. Die Anpassungsfähigkeit (Plastizität) des Nervensystems. *Hb. norm. pathol. Physiol.*, 15: 1045–1130.

Bielschowsky, A. 1940. *Lectures on Motor Anomalies*. Dartmouth College Publications, Hanover, N. H.

Billig, H. E., and A. van Harreveld. 1943. A new aspect of muscle reinnervation. *U. S. nav. med. Bull.*, 41: 410–414.

Billington, R. W. 1922. Tendon transplantation for musculospiral (radial) nerve injury. *J. Bone Joint Surg.*, 4: 538–547.

Bishop, G. H. 1944. The structural identity of the pain spot in human skin. *J. Neurophysiol.*, 7: 185–198.

Blalock, A., and S. J. Crowe. 1926. The recurrent laryngeal nerve in dogs. *Arch. Surg.*, 12: 95–116.

Boeke, J. 1935. Nervenregeneration. *Hb. Neurologie*, 1: 995–1122. (Julius Springer.)

Boring, E. G. 1916. Cutaneous sensation after nerve division. *Quart. J. exp. Physiol.*, 10: 1–95.

Brenner, C. 1944. Injuries to peripheral nerves; a review of recent literature. *War Med.*, 5: 21–35.

Bristow, R. 1941. Discussion on injuries to peripheral nerves. *Proc. R. Soc. Med.*, 34: 513–532.

Brunner, H. 1926. Ueber plastische Operationen bei Facialislähmung. *Arch. klin. Chir.*, 140: 85–100.

Burget, G. E. 1917. Attempts to produce experimental thyroid hyperplasia. *Amer. J. Physiol.*, 44: 492–503.

Buzzard, E. F. 1921. Prognosis in peripheral nerve injuries. In *Orthopedic Surgery of Injuries*. (Ed. by Jones.) 2: 139–143.

Cairns, H., and J. Z. Young. 1940. Treatment of gunshot wounds of peripheral nerves. *Lancet*, 2: 123–125.

Cajal, S. R. 1928. *Degeneration and Regeneration of the Nervous System*. Oxford University Press, London.

Calugareanu, and Henri. 1901. Régéneration fonctionnelle de la corde du tympan suturée avec le bout central du nerf hypoglosse. *C. R. Soc. Biol., Paris*, p. 1099.

Cannon, W. B., C. A. L. Binger, and R. Fitz. 1914. Experimental hypertension. *Amer. J. Physiol.*, 36: P363–364.

——, and R. Fitz. 1916. Further observations on over-activity of the cervical sympathetic. *Amer. J. Physiol.*, 40: P126.

——, and H. Haimovici. 1939. The sensitization of motoneurones by partial "denervation." *Amer. J. Physiol.*, 126: 731–740.

Clark, D. A. 1931. Muscle counts of motor units: a study in innervation ratios. *Amer. J. Physiol.*, 96: 296–304.

Clawthorne, T. 1941. Discussion on the limitations of operative treatment in traumatic facial paralysis. *Proc. R. Soc. Med.*, 34: 575–584.

Codivilla, A. 1904. Meine Erfahrungen über Sehnenverpflanzungen. *Z. orthop. Chir.*, 12: 221–251.

Coleman, C. C. 1920. The interpretation of muscle function in its relation to injuries of the peripheral nerves. *Surg. Gynaec. Obstet.*, 31: 246–254.

——. 1940. Results of facio-hypoglossal anastomosis in the treatment of facial paralysis. *Ann. Surg.*, 111: 958–970.

——. 1941. War wounds of the nervous system. *Ann. Surg.*, 113: 712–719.

——. 1944a. Surgical treatment of peripheral nerve injuries. *Surg. Gynaec. Obstet.*, 78: 113–124.

——. 1944b. Surgical lesions of the facial nerve: with comments on its anatomy. *Ann. Surg.*, 119: 641–655.

Colledge, L. 1925. On the possibility of restoring movement to a paralysed vocal cord by nerve anastomosis. *Brit. med. J.*, 1: 547–548.

——, and C. Ballance. 1927. The surgical treatment of paralysis of the vocal cord and of paralysis of the diaphragm. *Brit. med. J.*, 1: 553–559, 609–612.

——, and ——. 1928. Anastomosis between the recurrent laryngeal and phrenic nerves. *Brit. med.* J., 1: 746–747.

Collier, D. J. 1940. Facial paralysis and its after treatment. *Lancet*, 2: 91–94.

——. 1941. Discussion on the limitations of operative treatment in traumatic facial paralysis. *Proc. R. Soc. Med.*, 34: 575–584.

Cooksey, F. S. 1941. Discussion on the limitations of operative treatment in traumatic facial paralysis. *Proc. R. Soc. Med.*, 34: 575–584.

Cordero, N., and A. J. Carlson. 1927. The effects of functional union of the central end of the phrenic nerve with the peripheral end of the motor nerve to the sternohyoid muscle. *Amer. J. Physiol.*, 82, 580–582.

Creed, R. S. 1931. The physiological integration of sensory processes within the grey matter of the nervous system: a critical review. *Brain*, 54: 29–54.

Cunningham, R. H. 1898. The restoration of coördinated volitional movement after nerve "crossing." *Amer. J. Physiol.*, 1: 239–254.

Cushing, H. 1903. The surgical treatment of facial paralysis by nerve anastomosis. *Ann. Surg.*, 37: 641–659.

Dale, H. H. 1935. Pharmacology and nerve endings. *Proc. R. Soc. Med.*, 28: 319–332.

Dallenbach, K. M. 1931. Nerve regeneration: the two-point limen. *Psychol. Bull.*, 28: 214.

Dane, P. G. 1921. The results of ninety-eight cases of nerve suture. *Brit. med. J.*, 1: 885–886.

Davis, J. S., and E. A. Kitlowski. 1934. General sensations in pedunculated flaps of skin. *Arch. Surg.*, 29: 982–1000.

Deanesly, E. 1913. Two cases of facio-hypoglossal nerve anastomosis. *Brit. med. J.*, 1: 1055.

Denny-Brown, D. 1929. On the nature of postural reflexes. *Proc. Roy. Soc., Lond.*, 104: 252–301.

——. 1929. The histological features of striped muscle in relation to its functional activity. *Proc. Roy. Soc., Lond.*, 104: 371–411.

Dijkstra, C. 1933. Die De- und Regeneration der sensiblen Endkörperchen des Entenschnabels (Grandry- und Herbst-Körperchen) nach Durchschneidung des Nerven, nach Fortnahme der ganzen Haut und nach Transplantation des Hautstückchens. *Z. mikr.-anat. Forsch.*, 34: 75–158.

Dogliotti, A. M. 1935. Études expérimentales et première application clinique d'une nouvelle opération destinée à augmenter et à équilibrer la fonction neuromusculaire dans la paralysie partielle des nerfs. *J. Chir.*, 45: 30–48.

Douglas, B., and L. H. Lanier. 1934. Changes in cutaneous localization in a pedicle flap. *Arch. Neurol. Psychiat.*, 32: 756–762.

Duel, A. B. 1932. Clinical experiences in surgical treatment of facial palsy by autoplastic nerve grafts. *Arch. Otolaryngol.*, 16: 767–788.

——. 1933. History and development of the surgical treatment of facial palsy. *Surg. Gynaec. Obstet.*, 56: 382–390.

Dunn, N. 1920. The causes of success and failure in tendon transplantation. *J. orthop. Surg.*, 2: 554–557.

Dusser De Barenne, J. G., and A. De Kleyn. 1928. Ueber vestibulären Nystagmus nach Exstirpation von allen sechs Augenmuskeln beim Kaninchen; Beitrag zur Wirkung und Innervation des Musculus retractor bulbi. *Pflüg. Arch. ges. Physiol.*, 221: 1–14.

Elsberg, C. A. 1917. Experiments on motor nerve regeneration and the direct neurotization of paralysed muscles by their own and by foreign nerves. *Science*, 45: 318–320.

Erlanger, J. 1905. On the union of a spinal nerve with the vagus nerve. *Amer. J. Physiol.*, 13: 372–395.

Ewert, P. H. 1930. A study of the effect of inverted retinal stimulation upon spatially coordinated behavior. *Genet. Psychol. Monogr.*, 7: 177–363.

——. 1936. Factors in space localization during inverted vision. I. Interference. *Psychol. Rev.*, 43: 522–546.

——. 1937. Factors in space localization during inverted vision. II. An explanation of interference and adaptation. *Psychol. Rev.*, 44: 105–116.

Feiss, H. O. 1911. Recent experimental work on the "fusion" of nerves and its practical bearing on infantile paralysis. Report of a case of infantile paralysis treated by this method. *Bost. med. surg. J.*, 164: 667–671.

——. 1912. Experimental studies of paralyses in dogs after mechanical lesions in their spinal cords with a note on "fusion" attempted in the cauda equinas or the sciatic nerves. *J. comp. Neurol.*, 22: 99–129.

Floresco, N. 1901. Suture croissée des nerfs. *Arch. med. exper.*, 13: 552–556.

Flourens, M. P. 1828. Expériences sur la réunion ou cicatrisation des plaies de la Moelle épinière et des Nerfs. *Ann. Sci. Natur.*, Ser. 1, 13: 113–122.

Foerster, O. 1918. Die Symptomatologie und Therapie der Kriegsverletzungen der peripheren Nerven. *Dtsch. Z. Nervenheilk.*, 59: 32–172.

——. 1930. Restitution der Mobilität und Sensibilität. *Dtsch. Z. Nervenheilk.*, 115: 248–314.

Ford, F. R. 1933. Paroxysmal lacrimation during eating as a sequel of facial palsy (syndrome of crocodile tears). *Arch. Neurol. Psychiat.*, 29: 1279–1288.

——, and B. Woodhall. 1938. Phenomena due to misdirection of regenerating fibers of cranial, spinal, and autonomic nerves. Clinical observations. *Arch. Surg.*, 36: 480–496.

Forrester-Brown, M. 1920a. Discussion on end-results of injuries to the peripheral nerves treated by operation. *Brit. med. J.*, 2: 462–470.

——. 1920b. Difficulties in the diagnosis of nerve function. *Brit. J. Surg.*, 7: 495–501.

Fort, W. B. 1940. An experimental study of the factors involved in the establishment of neuromuscular connections. Dissertation, Univ. of Chicago.

Fowler, E. P. 1939. Abnormal movements following injury to the facial nerve. *J. Amer. med. Ass.*, 113: 1003–1008.

Frazier, C. H. 1924. The treatment of paralysis of the recurrent laryngeal nerve by nerve anastomosis. *Ann. Surg.*, 79: 161–171.

——, and W. B. Mosser. 1926. Treatment of recurrent laryngeal nerve paralysis by nerve anastomosis. *Surg. Gynaec. Obstet.*, 43: 134–139.

Fridberg, D. 1931. Das Auriculo-temporale Syndrom. *Dtsch. Z. Nervenheilk.*, 121: 225–239.

Gallinek, A. 1939. The phantom limb. *Amer. J. Psychiat.*, 96: 413–422.

Gellhorn, E., H. Gellhorn, and J. Trainor. 1931. The influence of spinal irradiation on cutaneous sensations. *Amer. J. Physiol.*, 97: 491–499.

Geohegan, W. A., and O. J. Aidar. 1942. Functional reorganization following preganglionectomy. *Proc. Soc. exp. Biol. Med.*, 50: 365–369.

Gill, A. B. 1921. End-results in the operative procedures for infantile paralysis, with special reference to tendon transplantation at the Widener Training School for Crippled Children. *J. orthop. Surg.*, 3: 677–689.

Gilmer, B. 1942a. The glomus body as a receptor of cutaneous pressure and vibration. *Psychol. Bull.*, 39: 73–93.

——. 1942b. The relation of cold sensitivity to sweat duct distribution and the neurovascular mechanisms of the skin. *J. Psychol.*, 13: 307–325.

Goldstein, K. 1939. *The Organism.* American Book Co., New York.

Gunn, M. 1886. The union of nerves of different functions considered in its pathological and surgical relations. *Trans. Amer. Surg. Ass.*, 4: 1–13.

Gutmann, E. 1942. Factors affecting recovery of motor function after nerve lesions. *J. Neurol. Psychiat.*, 5: 81–95.

——, and L. Guttmann. 1942. Factors affecting recovery of sensory function after nerve lesions. *J. Neurol. Psychiat.*, 5: 117–129.

——, and F. K. Sanders. 1942. Functional recovery following nerve grafts and other types of nerve bridge. *Brain*, 65: 373–408.

v. Hacker. 1914. Direkte Nerveneinpflanzung in den Muskel und muskuläre Neurotisation bei einem Falle von Cucullarislähmung. *Zbl. Chir.*, 41: 881–884.

Hamburger, V. 1928. Die Entwicklung experimentell erzeugter nervenloser und schwach innervierter Extremität. *Arch. Entwmech. Org.*, 114: 272–363.

Harris, W., and V. W. Low. 1903. On the importance of accurate muscular analysis in lesions of the brachial plexus. *Brit. med. J.*, 2: 1035–1038.

Hayward, E. 1917. Periphere Pfropfung des Musculo-cutaneous in den Medianus bei Plexusschussverletzung. *Zbl. Chir.*, 44: 263–265.

Head, H. 1920. *Studies in Neurology.* Vol. I. Oxford University Press, London.

Hebb, D. O. 1937. The innate organization of visual activity. II. Transfer of response in the discrimination of brightness and size by rats reared in total darkness. *J. comp. Psychol.*, 24: 277–299.

Highet, W. B. 1942. Procaine nerve block in the investigation of peripheral nerve injuries. *J. Neurol. Psychiat.*, 5: 101–129.

——. 1943. Innervation and function of the thenar muscles. *Lancet*, 1: 227–230.

——, and F. K. Sanders. 1943. The effects of stretching nerves after suture. *Brit. J. Surg.*, 30: 355–369.

Hilgard, E. R., and D. G. Marquis. 1940. *Conditioning and Learning.* D. Appleton-Century, New York.

Hoessly, H. 1916. Ueber Nervensimplantation bei Recurrenslähmungen. *Beitr. klin. Chir.*, 99: 186–192.

Hoffmann, P. 1915. Ueber eine Methode, den Erfolg einer Nervennaht zu beurteilen. *Med. Klin.*, 11: 359–360; 856–858.

v. Hofmeister. 1915. Ueber doppelte und mehrfache Nervenpfropfung. *Beitr. klin. Chir.*, 96: 329–390.

Howe, H. A., S. S. Tower, and A. B. Duel. 1937. Facial tic in relation to injury of the facial nerve. *Arch. Neurol. Psychiat.*, 38: 1190–1198.

Howell, W. H., and G. C. Huber. 1892. A physiological, histological and clinical study of the degeneration and regeneration in peripheral nerve fibres after severance of their connections with the nerve centre. *J. Physiol.*, 13: 335–406.

Hughes, D. M. 1918. Anomalous muscular action in nerve injuries. *Brit. med. J.*, 1: 720.

Ingham, S. D. 1920. Practical considerations in the diagnosis of peripheral nerve injuries, with special reference to compensatory movements. *Arch. Neurol. Psychiat.*, 3: 107–123.

Jackson, E. 1923. Transfer of function of the ocular muscles. *Amer. J. Ophthal.*, 6: 117–123.

Jianu, A. 1909. Die chirurgische Behandlung der Facialislähmung. *Dtsch. Z. Chir.*, 102: 377–386.

JONES, F. W. 1919. Voluntary muscular movements in cases of nerve lesions. *J. Anat.*, 54: 41–57.

JOYCE, D. 1920. Discussion on end-results of injuries to the peripheral nerves treated by operation. *Brit. med. J.*, 2: 462–470.

KAMINSKY, S. D. 1920. Ueber das Syndrom der Krokodils-Tränen. *Dtsch. Z. Nervenheilk.*, 110: 151–160.

KENNEDY, R. 1897. On the regeneration of nerves. *Philos. Trans. Roy. Soc. Lond.*, 188: 257–299.

——. 1899. On the restoration of co-ordinated movements after nerve section. *Trans. Roy. Soc. Edinb.*, 39: 685–702.

——. 1901. On the restoration of co-ordinated movements after nerve-crossing, with interchange of function of the cerebral cortical centres. *Philos. Trans. Roy. Soc. Lond.*, 194B: 127–162.

——. 1911a. Experiments on the restoration of paralysed muscles by means of nerve anastomosis. Part I. Substitutes for the facial nerve. *Philos. Trans. Roy. Soc. Lond.*, 202B: 93–163.

——. 1911b. Experiments on the restoration of paralysed muscles by means of nerve anastomosis. *Proc. Roy. Soc. Lond.*, 84B: 75–78.

——. 1914a. Experiments on the restoration of paralyzed muscles by means of nerve anastomosis. Part II. Anastomosis of the nerves supplying limb muscles. *Philos. Trans. Roy. Soc. Lond.*, 205B: 27–74.

——. 1914b. Experiments on the restoration of paralysed muscles by means of nerve anastomosis. Part II. Anastomosis of the nerves supplying limb muscles. *Proc. Roy. Soc. Lond.*, 87B: 331–335.

——. 1915. Experiments on the restoration of paralyzed muscles of means of nerve anastomosis. Part III. Anastomosis of the brachial plexus, with a consideration of the distribution of its roots. *Proc. Roy. Soc. Lond.*, 89B: 94–96.

——. 1919. On the prognosis of nerve injuries. *Lancet*, 2: 5–9.

KILVINGTON, B. 1905. An investigation on the regeneration of nerves. Part I. *Brit. med. J.*, 1: 935–940.

——. 1907. An investigation on the regeneration of nerves, with regard to surgical treatment of certain paralyses. *Brit. med. J.*, 1: 988–990.

——. 1912. An investigation on the regeneration of nerves, with regard to the surgical treatment of certain paralyses. Part V. *Brit. med. J.*, 1: 177–179.

——. 1941. Some experiments on nerve regeneration. *Aust. N. Z. J. Surg.*, 10: 266–272.

KÖLLIKER, T. 1917. Einflanzung eines Astes des N. medianus in den M. biceps nach Heineke. *Zbl. Chir.*, 44: 454.

KREDEL, F. E., and J. P. EVANS. 1933. Recovery of sensation in denervated pedicle and free skin grafts. *Arch. Neurol. Psychiat.*, 29: 1203–1221.

KROLL, M. 1929. *Die neuropathologischen Syndrome; zugleich Differentialdiagnostik der Nervenkrankheiten.* Julius Springer, Berlin.

KRUKENBERG. 1918. Die Kriegsverletzungen des Rückenmarkes. *Beitr. klin. Chir.*, 113: 246–249.

LANGLEY, J. N. 1898a. On the regeneration of preganglionic and of post-ganglionic visceral nerve fibers. *J. Physiol.*, 22: 215–230.

——. 1898b. On the union of cranial autonomic (visceral) fibres with the nerve cells of the superior cervical ganglion. *J. Physiol.*, 23: 240–270.

——. 1900. Notes on the regeneration of the preganglionic fibers in the sympathetic system. *J. Physiol.*, 25: 417–426.

——. 1908. Effect on nail growth and sensation of section of a cutaneous digital nerve, and effect on sensation of cocainizing a cutaneous nerve of the foot. *J. Physiol.*, 36 (suppl.): xlv.

——. 1918. On the separate suture of nerves in nerve trunks. *Brit. nerv. J.*, 1: 45–47.

——, and H. K. ANDERSON. 1904a. On the union of the fifth cervical nerve with the superior cervical ganglion. *J. Physiol.*, 30: 439–442.

——, and ——. 1904b. The union of different kinds of nerve fibres. *J. Physiol.*, 31: 365–391.

——, and M. HASHIMOTO. 1917. On the suture of separate nerve bundles in a nerve trunk and on internal nerve plexuses. *J. Physiol.*, 51: 318–346.

LANIER, L. H., H. M. CARNEY, and W. D. WILSON. 1935. Cutaneous innervation. *Arch. Neurol. Psychiat.*, 34: 1–60.

LASHLEY, K. S. 1921. Studies of cerebral function in learning. II. The effects of long continued practice upon cerebral localization. *J. comp. Psychol.*, 1: 453–468.

——. 1931. Mass action in cerebral function. In *Harvey Lectures*, 26: 46–67. Williams & Wilkins Co., Baltimore.

LEE, F. C. 1929. The regeneration of nervous tissue. *Physiol. Rev.*, 9: 575–623.

LEINFELDER, P. J., and N. M. BLACK. 1941. Experimental transposition of the extraocular muscles in monkeys. *Amer. J. Ophthal.*, 24: 1115–1120.

——, and ——. 1942. Experimental transposition of extraocular muscles in monkeys. *Amer. J. Ophthal.*, 25: 974–976.

LEVEUF, J., and A. PERROT. 1937. Les transplantations tendineuses dans le traitment des pièds bots paralytiques. *Rev. Orthop.*, 24: 393–448.

LEWIS, T. 1937. The nocifensor system of nerves and its reactions. *Brit. med. J.*, 1: 431–435; 491–494.

LIPSCHITZ. 1907. Ueber aberrierende Bündel bei Facialislähmung. *Neurol. Cbl.*, 26: 380–381.

Livingston, W. K. 1943. *Pain Mechanisms*. Macmillan Co., New York.

Manigk, W. 1934. Umstellung der Koordination nach Kreuzung der Achillessehnen des Frosches. *Pflüg. Arch. ges Physiol.*, 234: 176.

Maragliano, D. 1911. Nervenüberpflanzung von der einen Seite auf die entgegengesetzte. *Zbl. Chir.*, 38: 5–7.

——. 1912. Les anastomoses nerveuses contralatérales: au point de vue expérimentales et clinique. *Pr. méd.*, 20: 853–854.

Marble, H. C., E. Hamlin, and A. L. Watkins. 1942. Regeneration in the ulnar, median and radial nerves. *Amer. J. Surg.*, 55: 274–294.

Marina, A. 1912. Die Theorien über den Mechanismus der assoziierten Konvergenzund Seitwärtzbewegungen, studiert auf Grundlage experimenteller Forschungsergebnisse mittels Augenmuskeltransplantationen an Affen. *Dtsch. Z. Nervenheilk.*, 44: 138–162.

——. 1915. Die Relationen des Paläencephalons (Edinger) sind nicht fix. *Neurol. Cbl.*, 34: 338–345.

Marine, D., J. M. Rogoff, and G. N. Stewart. 1917. The influence on the thyroid of anastomosis of the phrenic and cervical sympathetic nerves. *Amer. J. Physiol.*, 45: 268–271.

Martin, R. C. 1940. Recent experiences with operation on the facial nerve. *Arch. Otolaryngol.*, 32: 1071–1075.

Meige, H., and Athanassio-Bénisty. 1916. Les signes cliniques des lésions de l'appareil sympathique et de l'appareil vasculaire dans les blessures des membres. *Pr. méd.*, 24: 157–160.

Mislavsky, M. 1902. Suture du sympathique cervical et du récurrent et centres corticaux du larynx. *C. R. Soc. Biol., Paris*, 54: 841.

Nafe, J. P. 1934. The pressure, pain, and temperature senses. In Murchison's *Handbook of General Experimental Psychology*, pp. 1037–1087. Clark University Press, Worcester.

Obrador, A. S. 1942a. Actividad refleja despues de la regeneracion y cruzamiento de nervios. *Bol. Lab. Est. Med. Biol., Mexico, D. F.*, 1: 223–226.

——. 1942b. Algunos problemas funcionales de la regeneracion nerviosa. *Ciencia*, 3: 300–304.

Olmsted, J., M. Margutti, and K. Yanagisawa. 1936. Adaptation to transposition of eye muscles. *Amer. J. Physiol.*, 116: 245–251.

Osborne, W. A. 1909. Epicritic regeneration. *Intercolon. med. J. Aust.*, 30: 99–100.

——, and B. Kilvington. 1908. Axon bifurcation in regenerated nerves. *J. Physiol.*, 37: 1–11.

——, and ——. 1910a. Central nervous response to peripheral nervous distortion. Part I. *Brain*, 33: 261–265.

——, and ——. 1910b. Central nervous response to peripheral nervous distortion. Part II. *Brain*, 33: 288–292.

Perthes, G. 1918. Ueber Sehnenoperationen bei irreparabler Radialislähmung, nebst Studien über die Sehnenverpflanzung und Tenodese im allegemeinen. *Beitr. klin. Chir.*, 113: 289–368.

——. 1922. Functionsrückkehr nach der Nervennaht. *Hb. Arzt. Erfahr. Weltkrieg, Leipzig*, 2: 580–596.

Phillips, G. 1938. The treatment of clonic facial spasm by nerve anastomosis. *Med. J. Aust.*, 25: 624–626.

Pitres. 1916. La valeur des signes cliniques permettant de reconnaître dans les blessures des nerfs periphiques. *Rev. neurol.*, 29: 477.

Pollock, L. J. 1919. Supplementary muscle movements in peripheral nerve lesions. *Arch. Neurol. Psychiat.*, 2: 518–531.

——. 1920a. The clinical signs of nerve injury and regeneration. *Surg. Gynaec. Obstet.*, 30: 472–480.

——. 1920b. Nerve overlap as related to the relatively early return of pain sense following injury to the peripheral nerves. *J. comp. Neurol.*, 32: 357–378.

——. 1922. Accessory muscle movements in deltoid paralysis. *J. Amer. med. Ass.*, 79: 526–528.

——, and L. Davis. 1933. *Peripheral Nerve Injuries*. Paul B. Hoeber, New York.

Purdy, D. M. 1934. Tactual space perception in translocated tissue. *J. gen. Psychol.*, 10: 227–229.

Rawa, A. L. 1885. Ueber das Zusammenwachsen der Nerven vershiedener Bestimmungen und vershiedener Functionen. *Arch. Physiol.*, pp. 296–328.

Reichert, E. T. 1885. Observations on the regeneration of the vagus and hypoglossal nerves. *Amer. J. med. Sci.*, 89: 146–159.

Riddoch, G. 1941. Phantom limbs and body shape. *Brain*, 64: 197–222.

Ritter, R. O. 1928. Transplantation of hamstring tendons forward to patella for paralysis of quadriceps extensor. *Ill. Med. J.*, 54: 284.

Rothman, S. 1941. Physiology of itching. *Physiol. Rev.*, 21: 357–381.

Sanders, F. K. 1942. The repair of large gaps in the peripheral nerves. *Brain*, 65: 281–337.

——, and J. Z. Young. 1942. The degeneration and reinnervation of grafted nerves. *J. Anat.*, 76: 143–166.

Sargent, P. 1920. Discussion on end-results of injuries to the peripheral nerves treated by operation. *Brit. med. J.*, 2: 462–470.

Schafer, E. S. 1919. Experiments on the cervical vagus and sympathetic. *Quart. J. exp. Physiol.*, 12: 231–301.

——. 1927. Recovery after severance of cutaneous nerves. *Brain*, 50: 538–547.

——. 1928. The effects of de-nervation of a cutaneous area. *Quart. J. exp. Physiol.*, 19: 85–107.

Scherb, R. 1927. Ueber die Gesetzmässigkeit der functionellen Umstellung von Muskeln nach Transplantation ihrer Sehnen. V. Mitteilung zur Myokinesigraphie. *Z. orthop. Chir.*, 48: 582–592.

——. 1928a. Functionelle Umstellbarkeit, Hemmung und Reparation antagonistisch gebundener Muskeln bei Poliomyelitis, ihre Bedeutung für die Sehnentransplantation und ihre biologische Gesetzmässigkeit. VI. Mitteilung zur Myokinesigraphie. *Z. orthop. Chir.*, 50: 470–493.

——. 1928b. Der Anteil der propriozeptiven Sensibilität an den funktionelle Umstellungsbedingungen bei Sehnentransplantation. Nachtrag zur VI. Mitteilung uber Myokinesigraphie. *Z. orthop. Chir.*, 52: 117–127.

——. 1938. Zur Sehnentransplantation bei poliomyelitischen Lähmungen. *Schweiz. med. Wschr.*, 19: 354–360.

Schiff, M. 1885. Réunion des nerfs moteurs d'origine et de fonctions différentes. *Arch. Sci. physiq. natur.*, 13: 202–211.

Seddon, H. J. 1942. A classification of nerve injuries. *Brit. med. J.* 2: 237–239.

v. Senden, M. 1932. *Raum- und Gestaltauffassung des operierten Blindgeborenen vor und nach der Operation.* Barth, Leipzig.

Sherren, J. 1906a. The distribution and recovery of peripheral nerves studied from instances of division in man. *Lancet*, 1: 727–733.

——. 1906b. Some points on the surgery of the peripheral nerves. *Edinb. med. J.*, 20: 297–332.

Sherrington, C. S. 1906. *The Integrative Action of the Nervous System.* C. Scribner's Sons, New York.

Sick, C., and A. Saenger. 1897. Heilung einer in Folge traumatischen Defects bedingten Lähmung des Radialis durch Vernähung des peripheren Endes dieses Nerven mit dem Medianus. *Arch. klin. Chir.*, 54: 271–279.

Speidel, C. C. 1942. Studies of living nerves. VIII. Histories of nerve endings in frog tadpoles subjected to various injurious treatments. *Proc. Amer. Philos. Soc.*, 85: 168–182.

Sperry, R. W. 1939. The functional results of muscle transposition in the hind limb of the rat. *Anat. Rec.*, 73 (suppl.): 51.

——. 1940. The functional results of muscle transposition in the hind limb of the rat. *J. comp. Neurol.*, 73: 379–404.

——. 1941. The effect of crossing nerves to antagonistic muscles in the hind limb of the rat. *J. comp. Neurol.*, 75: 1–19.

——. 1942a. Transplantation of motor nerves and muscles in the forelimb of the rat. *J. comp. Neurol.*, 76: 283–321.

——. 1942b. Fixed persistence in the rat of spinal reflex patterns rendered extremely maladaptive by cross union of sensory nerves. *Anat. Rec.*, 84: 483.

——. 1943a. Functional results of crossing sensory nerves in the rat. *J. comp. Neurol.*, 78: 59–90.

——. 1943b. Effect of 180 degree rotation of the retinal field on visuomotor coördination. *J. exp. Zool.*, 92: 263–279.

——. 1943c. Visuomotor coordination in the newt (*Triturus viridescens*) after regeneration of the optic nerve. *J. comp. Neurol.*, 79: 33–55.

——. 1944. Optic nerve regeneration with return of vision in anurans. *J. Neurophysiol.*, 7: 57–69.

——. 1945. Restoration of vision after crossing of the optic nerves and after contralateral transplantation of the eye. (In press.)

Spiegel, E. A., and T. D. Démétriades. 1925. Die zentrale Kompensation des Labyrinthverlustes. *Pflüg. Arch. ges. Physiol.*, 210: 215–222.

Spiller, W. G. 1919. Contracture occurring in partial recovery from paralysis of the facial nerve and other nerves. *Arch. Neurol. Psychiat.*, 1: 564–566.

Spitzy, H. 1904. Bie Bedeutung der Nervenplastik für die Orthopädie. *Z. orthop. Chir.*, 13: 326–355.

——. 1905. Weitere Erfahrungen auf dem Gebiete der Nervenplastik. *Z. orthop. Chir.*, 14: 671–684.

——. 1907. Die Anwendung der Lehre von der Regeneration und Hielung durchschnittener Nerven in der chirurgischen Praxis. *Wien. klin. Wschr.*, 20: 1493–1500.

——. 1908. Zur Frage der Behandlung von Lähmungen mittels Nervenplastik. *Münch. med. Wschr.*, 55: 1423–1426.

Stefani, A. 1886. Die Verheilung von Nerven benutzt zum Studium der Functionen der Nervencentren. *Arch. Physiol.*, p. 488–499.

Steindler, A. 1919. Report on 48 cases of tendon transplantation of the foot. Physiological method. *J. orthop. Surg.*, 1: 187–197.

——. 1940. *Orthopedic Operations, Indications, Technique and End Results.* Charles C. Thomas, Springfield, Illinois.

Stewart, D. 1937. Variations from normal gait after muscle section in rabbits. *J. Anat.*, 72: 101–108.

Stewart, J. E. 1925. An experimental study of the transplantation of the nerve supply of muscles. *J. Bone Joint Surg.*, 23: 948–956.

Stiles, H. J., and M. F. Forrester-Brown. 1922. *Treatment of Injuries of the Peripheral Spinal Nerves.* Frowde and Hadder & Stoughton, London.

Stone, L., and W. Jenkins. 1940. Recent research in cutaneous sensitivity: I. Pain and temperature. *Psychol. Bull.*, 37: 285–311.

Stone, L. S., and I. S. Zaur. 1940. Reimplantation and transplantation of adult eyes in the salamander (*Triturus viridescens*) with return of vision. *J. exp. Zool.*, 85: 243–269.

Stookey, B. 1922. *Surgical and Mechanical Treatment of Peripheral Nerves.* W. B. Saunders Co., Philadelphia.

Stopford, J. S. B. 1926. An explanation of the two-stage recovery of sensation during regeneration of a peripheral nerve. *Brain*, 49: 372–386.

——. 1927. Disturbances of sensation following section and suture of a peripheral nerve. *Brain*, 50: 391–398.

——. 1930. *Sensation and the Sensory Pathway.* Longmans, Green and Co., New York.

Storr, C. L. 1922. Army experiences with tendon transference. *J. Bone Joint Surg.*, 4: 3–21.

Stracker, O. 1919a. Ergebnisse der Operationen an den peripheren Nerven. *Beitr. klin. Chir.*, 116: 244–270.

Stratton, G. M. 1896. Some preliminary experiments on vision without inversion of the retinal image. *Psychol. Rev.*, 3: 611–617.

——. 1897. Vision without inversion of the retinal image. *Psychol. Rev.*, 4: 341–360; 463–481.

Swan, R. H. 1918. Surgical treatment of peripheral nerve injury and its results. *Arch. radiol. electroth.*, 23: 62–66.

Taylor, A. C. 1944. Selectivity of nerve fibers from the dorsal and ventral roots in the development of the frog limb. *J. exp. Zool.*, 96: 159–185.

Taylor, F. V. 1936. The effect of transposition of the Achilles tendon on the walking and righting movements of the frog. *J. comp. Psychol.*, 21: 245–273.

Thorburn, W. 1920a. On the end-results of peripheral nerve injuries treated by operation. *Lancet*, 2: 640–643.

——. 1920b. Discussion on end-results of injuries to the peripheral nerves treated by operation. *Brit. med. J.*, 2: 462–470.

Tower, S. S. 1940. Unit for sensory reception in the cornea with notes on nerve impulses from sclera, iris and lens. *J. Neurophysiol.*, 3: 486–500.

——. 1943. Pain: definition and properties of the unit for sensory reception. *Res. Publ. Ass. Res. nerv. ment. Dis.*, 23: 16–43.

Trotter, W., and H. M. Davies. 1909. Experimental studies in the innervation of the skin. *J. Physiol.*, 38: 134–246.

——, and ——. 1913. The peculiarities of sensibility found in cutaneous areas supplied by regenerating nerves. *J. Psychol. Neurol.*, 20: 102–150.

Tubby, A. H. 1906. Recent surgical methods in the treatment of certain forms of paralysis. *Brit. med. J.*, 1: 481–488.

Uprus, V., J. B. Gaylor, and E. A. Carmichael. 1934. Localized abnormal flushing and sweating on eating. *Brain*, 57: 443–453.

Vinke, T. H. 1934. Myokinetic studies of transplanted muscles about the knee. *Arch. Surg.*, 29: 345–364.

Walshe, F. M. R. 1942. The anatomy and physiology of cutaneous sensibility: A critical review. *Brain*, 65: 48–112.

Watrous, W. G., and J. M. Olmsted. 1940. Reflex studies after muscle transplantation. *Amer. J. Physiol.*, 132: 607–611.

——, and ——. 1941. Some reflex effects of nerve crossing and nerve regeneration. *J. comp. Neurol.*, 75: 21–37.

Weddell, G. 1941a. The pattern of cutaneous innervation in relation to cutaneous sensibility. *J. Anat.*, 75: 346–367.

——. 1941b. The multiple innervation of sensory spots in the skin. *J. Anat.*, 75: 441–446.

——. 1941c. The clinical significance of the pattern of cutaneous innervation. *Proc. Roy. Soc. Med.*, 34: 776–778.

——. 1942. Axonal regeneration in the cutaneous nerve plexuses. *J. Anat.*, 77: 49–62.

——, and P. Glees. 1942. The early stages in the degeneration of cutaneous nerve fibres. *J. Anat.*, 76: 65–93.

——, L. Guttmann, and E. Gutmann. 1941. The local extension of nerve fibers into denervated areas of skin. *J. Neurol. Psychiat.*, 4: 206–225.

Weiss, P. 1935. Homologous (resonance-like) function in supernumerary fingers in a human case. *Proc. Soc. exp. Biol. Med.*, 33: 426–430.

——. 1936. Selectivity controlling the central-peripheral relations in the nervous system. *Biol. Rev.*, 11: 494–531.

——. 1937a. Further experimental investigations on the phenomenon of homologous response in transplanted amphibian limbs. II. Nerve regeneration and the innervation of transplanted limbs. *J. comp. Neurol.*, 66: 481–535.

——. 1937b. Further experimental investigations on the phenomenon of homologous response in transplanted amphibian limbs. IV. Reverse locomotion after the interchange of right and left limbs. *J. comp. Neurol.*, 67: 269–315.

——. 1941a. Does sensory control play a constructive role in the development of motor coordination? *Schweiz. med. Wschr.*, 71: 591–595.

——. 1941b. Nerve patterns: the mechanics of nerve growth. *Third Growth Symposium*, 5: 163–203.

——. 1941c. Self-differentiation of the basic patterns of coordination. *Comp. Psychol. Monogr.*, 17, no. 4: p. 96.

——. 1942. Lid-closure reflex from eyes transplanted to atypical locations in *Triturus torosus:* Evidence of a peripheral origin of sensory specificity. *J. comp. Neurol.*, 77: 131–169.

——. 1943a. Nerve regeneration in the rat following tubular splicing of severed nerves. *Arch. Surg.*, 46: 525–547.

—. 1943b. Nerve reunion with sleeves of frozen-dried artery in rabbits, cats and monkeys. *Proc. Soc. exp. Biol. Med.*, 54: 274–277.

—. 1943c. Functional nerve regeneration through frozen-dried nerve grafts in cats and monkeys. *Proc. Soc. exp. Biol. Med.*, 54: 277–279.

—, and P. Brown. 1941. Electromyographic studies on recoordination of leg movements in poliomyelitis patients with transposed tendons. *Proc. Soc. exp. Biol. Med.*, 48: 284–287.

—, and T. C. Ruch. 1936. Further observations on the function of supernumerary fingers in man. *Proc. Soc. exp. Biol. Med.*, 34: 569–570.

—, and A. C. Taylor. 1943a. Repair of peripheral nerves by grafts of frozen-dried nerve. *Proc. Soc. exp. Biol. Med.*, 52: 326–328.

—, and ——. 1943b. Histomechanical analysis of nerve reunion in the rat after tubular splicing. *Arch. Surg.*, 47: 419–447.

Woods, A. H. 1919. Misleading motor symptoms in the diagnosis of nerve wounds. *Arch. Neurol. Psychiat.*, 2: 532–538.

Wright, A. D. 1941. Discussion on the limitations of operative treatment in traumatic facial paralysis. *Proc. R. Soc. Med.*, 34: 575–584.

Young, J. Z. 1941. Discussion on the limitations of operative treatment in traumatic facial paralysis. *Proc. Roy. Soc. Med.*, 34: 575–584.

——. 1942. The functional repair of nervous tissue. *Physiol. Rev.*, 22: 318–374.

——, and P. B. Medawar. 1940. Fibrin suture of peripheral nerves. *Lancet*, 2: 126–128.

Young, P. T. 1928. Auditory localization with acoustical transposition of the ears. *J. exp. Psychol.*, 11: 399–429.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* The Quarterly Review of Biology, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

What Is Life? and What Is Truth?

A review of *What Is Life? The Physical Aspect of the Living Cell.* Based on a course of public lectures delivered under the auspices of the Institute for Advanced Studies at Trinity College, Dublin, Ireland, in February, 1943. By *Erwin Schrödinger. Cambridge, England* (Cambridge University Press) and *New York* (The Macmillan Company). $1.75. viii + 91 pages; plates. 1945.

By Max Delbrück, Department of Physics, Vanderbilt University.

The author of this little book proposes to discuss the large and important question: "How can the events *in space and time* which take place within the spatial boundary of the living organism be accounted for by physics and chemistry."

This is a broad question, embracing the problem content of many branches of the biological sciences. Biologists with a romantic reverence for the powers of modern physics might be led to expect great revelations from the book. It turns out, however, that the author's aims are much more modest. It is not at all in the "how" of the accounting that the author is interested but in the question *whether* physics and chemistry will be able to give a *complete* account. This is not so clear-cut a question as might appear, since the terms physics and chemistry are ill-defined when applied not to the present but to the future content of these sciences. It is also a question whose answer involves prophecy, and there is not much point in arguing about prophecy. In his main discussion the author therefore climbs down to a still more modest ground and defines as his aim the establishment of this point of view:

"The obvious inability of present-day physics and chemistry to account for such events is no reason at all for doubting that they can be accounted for by those sciences."

The argument runs as follows:

In physics we have learned to describe the well determined behavior of systems by two types of law. Either the systems are made up of large solid bodies, like clocks, and follow dynamical laws unperturbed by molecular heat motion; or they are made up of very large numbers of statistically independent elements, and observation concerns the average behavior of these elements. We are then dealing with statistical laws that appear to be accurate laws because the numbers of particles involved are so large that statistical fluctuations are negligibly small. The diffusion law and the mass action law are examples of this type of law in which "order comes from disorder." In either of these two types of well determined behavior, it is essential that individual molecules should have no measurable effect on observable quantities.

Being well acquainted with this situation, the naive physicist would expect that the living cell, exhibiting a well determined behavior, is constructed on the same principles, i.e., that it functions like a clock or like a thermal machine, or some mixture of the two. In any event, he would expect it to be well protected from being thrown off balance by statistical fluctuations. Therefore, if the cell contains molecular species with an important rôle in its makeup, he would expect each such molecular species to be represented by a very large number of individual molecules. In these expectations the naive physicist finds himself flatly contradicted by the facts of life. Far from being a mass action system, either in the dynamic or in the thermodynamic sense, the living cell is controlled by genes which are present in single or double copy, and which are handed on from cell to cell by an unknown mechanism of reproduction.

This outline of the naive physicist's dilemma is followed by an exposition of some of the elements of genetics, of the results of radiation genetics, and of other data bearing on the mechanism of mutation and on the stability of the genes. The discussion leads up to the concept of the gene as an "aperiodic crystal." The genes are given this startling name rather than the current name " complicated molecule," because the author wishes to emphasize, first, that the stability of the genes is of the same kind as the stability of crystals in which the constituent atoms are held together by valency bonds, and second, that these crystals are of a new kind, not previously investigated by physicists who concentrated their attention on periodic crystals. There is nothing new in this exposition, to which the larger part of the book is devoted, and biological readers will be inclined to skip it.

Schrödinger lays great stress on the fact that the stability of the genes is a quantum mechanical stability. We know that the stability of atoms and molecules is deeply rooted in quantum mechanics, and our general understanding of molecular stability has been of help when the stability of genes was investigated. This indebtedness to quantum mechanics is not a private debt of biology. It is part of the general debt of chemistry to quantum mechanics. In Schrödinger's opinion, the dependence of the well determined behavior of living organisms on this new and little studied physical structure, the "aperiodic crystal," explains the obvious inability of present day physics and chemistry to account for this behavior. In his opinion the inability is similar to the inability of a man who knows how a steam engine works and who is confronted with an electric generator. Both of these contraptions contain iron and copper, but unless he has studied electrical phenomena the steam engineer will be quite unable to understand the working of the generator. He might be tempted to believe that the laws of physics break down when applied to the generator, while in reality he is merely confronted with the behavior of matter under a new set of conditions which he has not yet analyzed.

This bold analogy will seem very suggestive to many readers. But is it a valid analogy? One must note that it is based in large measure on a substitution of terms. For the term "complicated molecule" he substitutes the term "aperiodic crystal," the latter term implying a new and unexplored state of matter.

After this profession of faith in the physical nature of the workings of the cell, Schrödinger attempts a further characterization of its mechanism, as one which produces order from order, in contradistinction to the statistical mechanism where the orderliness of the observed phenomena is the result of the disorder of the molecules. The clockwork is also based on the order from order principle. The basic similarity between the clock and the living cell is seen in the fact that both depend on the solidity of the controlling parts, the clockwork on massive, man-made solids, the cell on the aperiodic crystalline genes. The essential difference between the clock and the living cell is seen in the fact that in the clock the disordering tendencies are kept at bay by operating with solids of large mass, while in the living cell the decay to thermodynamic equilibrium is evaded by continually drawing on sources of negative entropy from its environment.

While it is of course correct to say that life processes depend on the availability of negative entropy, such a statement is at best a partial description of the tricks of life. It fits any system of enzymes acting on their substrates. Translated into the usual terminology it reads: the living cell employs specific enzymes, and these enzymes promote selectively some of the reactions which involve an increase in free energy.

The author does not return in his later discussion to the problem of how the cell gets around the statistical fluctuations. The careful reader will be disappointed by this omission. At the beginning of the book the statistical fluctuations are represented as an unsurmountable obstacle to the physical understanding of the cell, but later on this difficulty seems forgotten. Without a finer discussion of this aspect, particularly for enzymatic processes and for non-steady states, the argument of the book loses its strength. How does the cell manage to produce just one replica of each gene at each cell division? Are we not here dealing with small numbers of molecules, and should we not expect large fluctuations? Perhaps, as some believe, more than one replica is formed, and the supernumerary ones are shed into the cytoplasm. But why do these extra pieces not cause havoc in the cytoplasm? How are the fluctuations in the numbers of these extra pieces brought under control? Perhaps our present knowledge of cellular processes is insufficient to make such a discussion convincing. If that be the case, then any statement about the physical nature of cellular organization would appear premature.

Schrödinger delimits his stand further by stating that, in his opinion, "and contrary to the opinion upheld in some quarters, *quantum indeterminacy* plays no biologically relevant role" (in the cell). The opinions here referred to are presumably those of Bohr and those of Jordan. This is not the place to take up the challenge for these authors, but it is to be hoped that they will themselves continue the discussion.

There is a brief epilogue on "Determinism and Free Will." Having declared his belief that the events in the cell, if not strictly deterministic, are at least statistico-deterministic, the author attempts in this epilogue to bring this belief into harmony with the "immediate experience" of a free will, i.e., with the experience of directing the motions of one's body, of which motions one foresees the effects. How can the conscious "I" direct something whose course is set by the laws of nature? Schrödinger thinks that the only solution to this dilemma lies in the assumption that the "I" and the laws of nature are one and the same thing. It must then be assumed that the "I" of immediate experience is a singular of which the plural is unknown. He draws on the scholars of the Vedanta and on other sources to support the view that the plurality of consciousness is an illusion. The reviewer finds himself unable to define his reaction to this epilogue.

Undoubtedly the book will attract many readers, because of its title, because of the very high respect which we owe to its author, and because of its clear, simple, and forceful style. It will have an inspiring influence by acting as a focus of attention for both physicists and biologists. Physicists will be interested in the book because it will to some extent answer their curiosity about biology. Biologists will find it hard to appreciate the dilemma of the "naive physicist" outlined at the beginning of the book. Physicists and biologists who are not familiar with Bohr's subtle complementarity argument will be inclined to take the physical nature of the cellular processes for granted at the outset, and may be dissatisfied because Schrödinger does not advance our understanding of cellular mechanisms in any specific respect. The reviewer believes, however, that Schrödinger's discussion of the types of laws of nature might exert a clarifying influence on biological thinking.

REVIEWS AND BRIEF NOTICES

GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

THE PHILOSOPHY OF BERTRAND RUSSELL. *The Library of Living Philosophers, Volume V.*
Edited by Paul Arthur Schilpp. Northwestern University, Evanston and Chicago. $4.00. xv + 815 pp. 1944.

In each volume of this "Library" some twenty exponents and opponents of the thought of an outstanding philosopher contribute expository or critical articles, and the philosopher himself submits a reply. There is also included an intellectual biography (or autobiography) of the thinker under discussion, along with a complete bibliography of his works. One very welcome result of such a project is to decrease the differences of opinion which inevitably arise as to what some of the profoundest writers of our age really intended to say.

The present volume is of special interest to scientists, because Russell came into philosophy from mathematics and has contributed to our understanding of the mathematical and other scientific methods of inquiry. Russell has tried to introduce "scientific method" into philosophy and has been a champion of the "empirical approach" to all but a few of the most abstract problems. He has also helped to work out the philosophical implications of some of the more striking scientific discoveries as well as the social implications of the scientific movement as a whole. Many of the authors pay tribute to other contributions of Russell to our age, notably, his inventions in the way of exact techniques for the attainment of the clarity and simplicity of thought for which he has such a passion, and his efforts in the interests of freedom, democracy, and social harmony.

Russell's critics very naturally call attention to the incompletenesses, confusions, and contradictions in his work and to the occasional failure of his theories to explain pertinent facts. Over-simplification is said to be inherent in his analytic and reductive tendencies, his ways of defining, his choice of indefinables, his search for a "minimum vocabulary," and his very assiduous use of "Occam's razor." He is also taken to task for creating "dualisms," for an occasional wavering between two irreconcilable trends of thought, and for an unreasonable amount of skepticism and pessimism. Some will think that the most serious charges levelled at him are: that his approach to social problems is "abstract and unhistorical"; that he misunderstands religion; and that his "ethical subjectivism" leaves him powerless before the onslaughts of a philosophy of power.

Russell very frankly acknowledges the justice of a few of these criticisms; and one feels that he successfully meets many of the remainder—either by new buttressings and extensions of his position or by showing that the charges arise from misinterpretations of what he has already said.

Russell's account of his intellectual development and his "Reply" afford many fascinating side-lights on his present stand, only a few of which can be mentioned here. Early in his career Russell deduced mathematics from logic; but now he believes that logic itself depends on psychology and physiology. A scientific account of reality, he holds, must employ both induction and deduction; but neither of these can be deduced from the other, and the principle of neither can at present be "proved." "The canons of scientific inference have never yet been formulated," he adds; "whether...an individual decides to accept or reject these canons, is a purely personal affair, not susceptible to argument..."

According to Russell, reality can be analysed into three kinds of "events": "unperceived events," sensations, and images. He contends that things, matter, electrons, waves, the self, etc., are merely series (or groups) of "events". In addition to "particulars," he thinks, at least one universal is essential to an adequate description of reality. The physical world, he holds, is best regarded as a four-dimensional manifold of "events"; and our knowledge of the physical world is merely a knowledge of "structure." Causal laws, he adds, may be assumed to be the same for living matter as for dead matter.

Russell believes that, although scientific laws are discoverable in the economic and statistical portions of history, there are determinants of the past other than the economic, so that we cannot expect to make history completely scientific. The knowledge that it gives of human beings, he maintains, is "not mainly analytic scientific knowledge, but the sort of knowledge a dog-lover has of his dog."

Science is ethically neutral, says Russell; it is a tool which cannot determine the purposes for which it should be used. It follows that science contains no basis for a belief in progress; and, since scientific method is the only rational method, that ethics has no rational basis. The good is simply the desired, he thinks; and a value judgment is merely an expression of a desire for something, together with a wish that all other persons have the same desire. Russell concedes that his social, political, and educational beliefs have no logical connection with his logic and epistemology; and he admits that these beliefs are just so much propaganda for democracy, freedom, and cooperation—which he personally happens to desire. It is at this point that he becomes defenseless, logically, against a philosophy of power.

To those who remember Russell's attitude toward religion in *Free Thought and Official Propaganda*, his announcement in this book that although religion does not represent truth, nevertheless "some form of personal religion is highly desirable," will come as something of a surprise. Similarly, his agreement with Einstein that "fear of metaphysics is the contemporary malady" may seem odd in view of his devotion to scientific method and his passion for simplicity.

As to trends, some of the expositors of Russell's thought find that it moves in the direction of empiricism and nominalism, while Russell himself remarks that in ontology he is becoming increasingly materialistic, and in theory of knowledge, increasingly subjectivistic.

It is of course foolish to expect agreement on a choice of contributors to a volume such as this; nevertheless, the omission of essays by such outstanding students of Russell's thought as John Dewey and Arthur O. Lovejoy—to mention only two of those who are conspicuous for their absence—will be disappointing to many. However, the volume is rewarding in a variety of ways and deserves a wide audience.

Raymond P. Hawes

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Principles of Modern Biology. *A Complete Reconstruction and Modernization of Charles R. Plunkett's Elements of Modern Biology.*

By Douglas Marsland. Henry Holt and Company, New York. $3.75. ix + 774 pp. 1945.

Being one of those who considered Plunkett's "Outline of Modern Biology" an outstanding textbook, the reviewer opened Marsland's revision of the 1930 edition with a mixture of hope and anxiety. Much of the hope and a little of the anxiety have been fulfilled.

The book has been completely reorganized. Instead of the first four parts, which consisted of chapters dealing with protoplasm, nutrition, response, and reproduction, there are now only three—on the cell, multicellular plants, and multicellular animals (with special emphasis on man). To the reviewer, this seems to be a more practical arrangement than the old for teaching, and the change is welcome. Equally welcome are the expansion of the single chapter on nutrition in multicellular animals (formerly of about 50 pages) into several chapters (now over 100 pages), dealing separately with digestion, metabolism, circulation, respiration, and excretion; and the inclusion of new material on such subjects as plant movements, viruses, hormones, and vitamins.

Unfortunately, there have been cuts as well as additions. One sad loss is incurred by the failure to include anything from the early edition on the determination of symmetry in development, another by omitting the section on the geographic distribution of organisms from the chapter on "The Results of Evolution"—a section which might well have been enlarged rather than eliminated. A number of photographs have been added to the text, and would doubtless enhance it had they not suffered from very poor reproduction—so poor that some of them are at present worthless. It is to be hoped that this will be corrected in later printings.

On the whole, though, it seems that the revision has brought Plunkett up to date fairly satisfactorily without sacrificing the stimulating quality of the earlier text, and the new Marsland and Plunkett deserves a trial.

Eileen Sutton Gersh

◆

The Book of From Seed to Tree.

The Book of Queer Animals. *Nature Science Books Outdoor Adventures.*

By Charles H. Gable and Ellen Schulz Quillin. Albert Whitman & Company, Chicago. 50 cents each. 48 pp.; 47 pp. 1944.

These stories about nature study are written for children of six to ten years, by a Texas public school teacher of nature study and science and the director of a museum in that state. Children will like them. There is an interesting attempt to encourage and illustrate scientific thinking. The account of photosynthesis in the first book listed is somewhat incorrect. The pictures appear crude in comparison with those in some other children's series.

ECOLOGY

Chemical Results of the Last Cruise of the Carnegie. *Scientific Results of Cruise VII of the Carnegie during 1928-1929 under Command of Captain J. P. Ault. Chemistry—I. Department of Terrestrial Magnetism, Carnegie Institution of Washington Publication 562.*

By Herbert W. Graham and Erik G. Moberg. Carnegie Institution of Washington, Washington. $1.25 (cloth); $1.00 (paper). vii + 58 pp. 1944.

This report considers the distribution in the sea of phosphate, silicate, hydrogen ions, and oxygen. The findings will be of considerable interest to ecologists and students of plant and animal distribution. The striking excess of phosphate and silicate in the Pacific as compared with the Atlantic, the deficiency of O_2 in the deep waters of the Pacific, and the strong negative correlation of phosphate concentration and pH are surely not without their important biological corollaries.

◆

Observation and Results in Physical Oceanography. *Scientific Results of Cruise VII of the Carnegie during 1928-1929 under Command of Captain J. P. Ault. Oceanography—I-A. Department of Terrestrial Magnetism, Carnegie Institution of Washington Publication 545.*

By H. U. Sverdrup, J. A. Fleming, F. M. Soule, C. C. Ennis. Carnegie Institution of Washington, Washington. $2.50 (cloth); $1.75 (paper). v + 156 pp. 1944.

This report deals mainly with determination of ocean depths, subsurface temperatures, densities, salinity, and the collection and preservation of bottom samples.

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I. Marine Bottom Samples Collected in the Pacific Ocean by the Carnegie on Its Seventh Cruise, *By Roger R. Revelle.* II. Radium Content of Ocean-Bottom Sediments, *by Charles S. Piggot. Scientific Results of Cruise VII of the Carnegie during 1928-1929 under Command of Captain J. P. Ault. Oceanography—II. Department of Terrestrial Magnetism, Carnegie Institution of Washington Publication 556.*

Carnegie Institution of Washington, Washington. $2.50 (cloth); $2.00 (paper). ix + 196 pp. 1944.

The description of marine bottom samples in this report has value for marine ecologists interested in the distribution of calcium carbonate in the Atlantic and Pacific Oceans, or of globigerina, radiolarian, and diatom oozes and muds. Other organic constituents of the samples include traces or minor amounts of sponge spicules, echinoid spines, and ostracod shells, and rare remains of bryozoan, molluscan, and vertebrate forms.

◆

The Genus Ceratium in the Pacific and North Atlantic Oceans. *Scientific Results of Cruise VII of the Carnegie during 1928-1929 under Command of Captain J. P. Ault. Biology—V. Department of Terrestrial Magnetism, Carnegie Institution of Washington Publication 565.*

By Herbert W. Graham and Natalia Bronikovsky. Carnegie Institution of Washington, Washington. $2.50 (cloth); $2.00 (paper). vii + 209 pp. 1944.

Fifty-eight species of *Ceratium*, including three new species, one new subspecies, and three new varieties, were collected by the "Carnegie" in the North Atlantic and Pacific Oceans. Their horizontal distribution seems to be unaffected by salinity or absolute phosphate content. Temperature is a more significant factor, the species (and subspecies) being divided into five groups: intolerant tropical (23); slightly tolerant tropical (23); very tolerant tropical (5); cosmopolitan (5); and subpolar (5). Currents are also certainly important. It is interesting that the eight rare solely Pacific species are either intolerant or slightly tolerant tropical species. It is noteworthy that tolerance of individual species may be decidedly different in the two oceans. The vertical distribution of *Ceratium* species was found, except for three species, to agree with Nielsen's theory of the deeper distribution of "shade forms" marked by thin, often expanded bodies crowded with chromatophores. The observed vertical migrations of Ceratia cannot be accounted for wholly by phototropism. The phototropism may itself depend on the supply and assimilation of certain nutrients. The figures and charts add to the value of this significant contribution to the study of plankton distribution.

EVOLUTION

Lamarck, *Interprete de la Naturaleza.*

By Enrique Beltran. Sociedad Mexicana de Historia Natural, Mexico, D. F. (Paper). xv + 161 pp. 1945.

This essay commemorating the 200th Anniversary of the birth of Lamarck, by a distinguished Mexican biologist who is professedly an admirer of the 'Founder of Evolution,' covers familiar ground for the most part. However, by removing Lamarck, the man, from the arena of subsequent struggles involving Lamarckism and neo-Lamarckism, a juster picture of the great evolutionist appears. The work of Lamarck is considered in relation to his epoch, the stormy years of the French Revolution with which he identified himself, to his forerunners, and to his contemporaries, the giants Buffon and Cuvier, whom, in historical perspective, the humble guardian of the king's herbarium was to eclipse. The author, who cleaves to neither of the Lamarckian schools in the controversial sense usually understood in biology, brings to date (1944) the status of 'lamarckismo,' that formidable rock in the evolutionary stream.

Excerpts from the works of Lamarck—'hidden treasures'—translated into Spanish, form the second half of this essay, to which a bibliography of Lamarck is appended.

H. R. Catchpole

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Experimental Studies on the Nature of Species. *II. Plant Evolution through Amphiploidy and Autoploidy, with Examples from the Madiinae. Carnegie Institution of Washington Publication 564.*

By Jens Clausen, David D. Keck, and William M. Hiesey. Carnegie Institution of Washington, Washington. $2.00 (cloth); $1.25 (paper). vii + 174 pp.; 4 plates. 1945.

This represents another invaluable contribution to the modern study of evolution. The first part of the study reports fully the results of investigations of three amphiploids, *Madia nutramii*, *M. citrigracilis*, and *Layia pentaglossa*. The first of these was artificially synthesized by a doubling of the chromosome number in the sterile hybrid between two geographically isolated species of *Madia*, differing in some fifty morphological characters as well as in chromosome number. Full fertility was attained by the amphiploid in the fourth generation. In the garden at Stanford, it exceeds both parents in vigor, and must be regarded as a good species, since it differs from all other species by characters of specific magnitude in the genus, reproduces only its own kind, and "is genetically isolated from all other species."

M. citrigracilis occurs as a natural species in a region where the distributions of *M. gracilis* and *M. citriodora* overlap. It has been resynthesized through hybridization of these two species, followed by a doubling of chromosome number in the highly infertile hybrid. *L. pentaglossa* is an artificial amphiploid similarly derived from *L. pentachaeta* and *L. platyglossa*. In one spot where the distributions of the parent species overlap, two similar natural amphiploid plants were found.

The second section of the book considers the place of amphiploidy in biosystematic relationships. The biosystematic units are defined as follows: The *ecotype* is a genetically and physiologically distinct ecologic race, there being no genetic obstacle to a free interchange of genes between ecotypes of the same species. The *ecospecies* manifests genetic barriers to the free interchange of genes with other ecospecies of the same cenospecies. The *cenospecies* is completely unable to exchange genes with other cenospecies of the same comparium, but by amphiploidy the genes of distinct cenospecies may be combined in a new species. The *comparium* is completely isolated from other comparia even by way of amphiploidy. The evolutionary processes are related to these levels in fundamental ways. Thus evolutionary processes initiated solely by hybridization, such as amphiploidy, chromosome exchange, or gene interchange, "have their best opportunities in comparia consisting of many cenospecies, with many ecospecies and ecotypes." The requirements for a successful amphiploid are outlined.

Experimental polyploids are then classified on these principles, in the most complete and well organized review available. Seventeen clear cases of amphiploids are grouped as either inter-ecospecific or inter-cenospecific, and it is made clear that the great majority of successful ones fall into the latter class, with parental genomes that show no inter-pairing and preserve their identity. Other examples of amphiploidy, in *Lactuca*, *Prunus*, and especially in *Rubus*, are reviewed, making 31 cases of ploidy in all.

In the next chapter the ecologic characteristics of eleven natural amphiploids are considered. It is found that in general they occur in environments intermediate between those occupied by the parent species, and in nearly half the cases appear to grow also in the habitats of their parents and become very successful. This chapter is followed by a similar consideration of ten natural autoploids. Simple doubling of all chromosomes in a plant may clearly enable the new form to occupy a new ecologic niche in some cases, and thereafter lead through selection to distinct diploid and tetraploid species. Changes from annual to perennial habit may result. Amphiploidy may be superimposed upon autoploidy.

The final chapter concludes with a summary of the authors' ideas regarding evolutionary sequence. The stages in this sequence are the ecotypes, ecospecies, cenospecies, and comparia. Amphiploidy has a rejuvenating effect, so that cenospecies may be reunited. "Youthful" groups have an abundance of ecotypes within a few ecospecies. A monotypic cenospecies in a single comparium is genetically "senescent." After the possibilities of amphiploidy and autoploidy are exhausted, apomixis may ensue. That is the final flare-up of variability in the group. Beyond this waits only extinction.

Every student of evolutionary problems will want to give this notable publication his deepest and most serious study.

Bentley Glass

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The Moral Theory of Evolutionary Naturalism.

By William F. Quillian, Jr. Yale University Press, *New Haven; Humphrey Milford, Oxford University Press, London.* $3.00. xiii + 154 pp. 1945.

It is quite natural that a book on the moral theory of evolutionary naturalism should begin by informing the reader what naturalism is, or at least what it is construed to be, as interpreted by the author. One is prone to think of the term as an antonym to supernaturalism. This implication is apparently accepted by the author, who refers to it as "that metaphysical view which holds that 'the universe requires no supernatural cause or government, but it is self-existent, self-explanatory, self-operating, and self-directing." It scarcely needs to be pointed out that there are many individuals eminent in the fields of science and philosophy who hold that all events in the universe transpire in accordance with natural laws and who would therefore consider themselves adherents of the doctrine of naturalism, but who entertain all sorts of views as to the metaphysical and the theological implications of this standpoint. With so many varieties of naturalism, opponents of this doctrine enjoy a considerable latitude in construing the term to suit themselves, and they have little difficulty in supporting their interpretations by quotations from authorities of high standing. After citing a statement by T. H. Huxley, Quillian tells us: "Thus, naturalism is seen to be that philosophical view which claims that the only knowledge we can have is of the world which is known through sense perception and which is the subject-matter of the natural sciences." Perhaps the author has overlooked Huxley's own emphatic rejection in his essay on Science and Morals of a very similar interpretation of his position made by Lilly. A naturalism which denies the possibility of knowledge of mathematics, of the psychology of reasoning, and of the moral emotions, because they are not known through sense perception, is a rather preposterous man of straw. But despite the author's unfortunate definition, his later discussions are not hampered by a strict adherence to it.

The second chapter, on "The Moral Theory of Evolutionary Naturalism," is chiefly expository of the views of Darwin, Spencer, Clifford, Leslie Stephen, Westermarck, and Guyau. In the following chapter, devoted to a criticism of this theory, the chief topics considered are the theories of the origin of the moral sense and the moral standards that have been derived from the fact of evolution. The arguments follow the usual line found in most of the many books and articles opposing a naturalistic ethics. It is conceded that "natural selection. . .has played an important part in the origin and development of primitive morality," but it is contended that "this naturalistic account. . .fails completely to explain the unique characteristics of the moral consciousness." The evolutionary naturalists are said to have fallen into the "genetic fallacy" which is based on "the belief that an adequate explanation of a phenomenon is rendered by tracing it to its origin." Even if the evolutionists can account for the way in which our moral sentiments have been evolved, "evolutionary ethics," we are told, "has fallen down just at the point where it tries to explain the nature and meaning of normative morality," which is concerned with "that which ought-to-be as distinguished from that which is." And normative morality is said to have "metaphysical foundations" which "have no place in a naturalistic theory of reality or of ethics."

The evolutionary moralists are accused of ignoring or explaining away the really essential features of the moral life. "If this 'nothing-but' point of view were true," Quillian asks, "what would be left of the moral life as we know it? There would be no moral judgments and no choice, for there would be no *understanding* of one's self or of other selves and of their relationships. . . .There would be no consciousness of obligation, no awareness of what I ought to be but am not."

Many writers on ethics seem to derive a peculiar satisfaction in portraying the dire consequences that would follow from consistent adherence to a purely naturalistic morality. Quillian's volume carries out this tradition in its usual form. The godless evolutionary naturalists have no adequate metaphysical ground for a normative morality, which "requires a criterion. . .adequate to account for the unconditional character of moral obligation. . . .What we call the moral law and values are abstractions which our limited and limiting minds make from the concreteness of the living God who is revealed."

Since this brief review is chiefly expository, I have refrained from commenting on many point concerning which I feel sure that most evolutionary naturalists would probably differ from the author.

S. J. HOLMES

NORTH AMERICAN PLEOSPONGIA. *Geological Society of America Special Papers, Number 48.*

By Vladimir J. Okulitch. The Geological Society of America, New York. $1.25 (paper). vii + 112 pp.; 18 plates. 1943.

Okulitch's monograph is an important step toward a fuller understanding of the nature of the exquisitely filigreed goblets from the Cambrian rocks, known to most geologists as the Archaeocyatidae or Pleospongia, even though the mystery of their origin and even of their biologic relationship is by no means entirely solved. Through recent researches these extinct organisms, typified by the genus *Archaeocyathus*, have grown in our understanding to the dignity of an extinct class of sedentary marine organisms. Okulitch (1937) suggested calling them Pleospongia, "to replace the indefinite term Archaeocyathi." He justifies this change because of the unanimity of the contemporary leading students of the group in rejecting the early belief in their affinity to corals, and in accepting their biologic relation to sponges, and particularly to calcareous sponges, as Okulitch concludes. While the arguments against a coral affinity of the Archaeocyathi, which he so well summarizes, are quite convincing, the suggested introduction of the class name Pleospongia in place of Archaeocyathi, through attractive phonetically, does not seem necessary taxonomically. Besides, the neutrality of the older term is an asset rather than a liability, and will continue to appeal to prudent scientific minds, a reminder of the fact that we are a long way yet from a wholly satisfactory biologic explanation of this as well as of many other fossil organisms. For instance, in the generally satisfactory formal classification of the Archaeocyathi, as worked out largely by Bedford, Vologdin, and Okulitch, we find a strange "Subclass Exocyatha," with its three families embracing five genera, whose suggested relationship to the rest of the class is biologically puzzling and therefore taxonomically quite arbitrary.

The opinions of the authorities on these growth forms, which are treated as "Exocyatha," differ widely. They develop as encrusting protean structures, which in details of anatomy resemble the ordinary cup-shaped Archaeocyathi, but depart radically from their rigid symmetrical shape. Some authors (Bedford) treat Exocyatha as an independent organism parasitic on ordinary Archaeocyathi, others (Taylor) believe that they are specialized structures of the latter for the purpose of anchoring them to the substratum; now Okulitch boldly suggests that they are pathologic outgrowths, somewhat comparable to cancer development in higher animals, but with a by far more vigorous and even "independent growth." To quote Okulitch's own words in this extraordinary explanation: "I believe that exothecal tissue is an outgrowth of central more regular archaeocyathid, that such tissue was capable of *independent growth* and secretion of skeletal elements, essentially similar to skeletal tissue of parent, and that main differences are due to lack of architectural boundaries, which were imposed on regular forms but not on the excrescences. It is quite likely that if a regular archaeocyathid became surrounded by its own exothecal tissue it might have become *stifled by it and died* for lack of food and water circulation. Thus great prolificity of growing pleospongian tissue may have contributed to their eventual extinction" (p. 84, italics added). Elsewhere he states that Exocyatha "may be a pathologic condition somewhat akin to cancerous growth of higher animals."

Perhaps some biologists will immediately dismiss the whole explanation as a flight of fantasy, but the general merit of Okulitch's work justifies an attempt at critical analysis and understanding of the facts and reasoning behind it. The striking similarity of the microstructure of the protean encrusting "Exocyatha" to the regularly cup-shaped Archaeocyathi upon which they grow seemingly indicates a common biologic nature, and obviously inspired the view that in this growth the organism suddenly freed itself from the "architectural" bonds of its radial symmetry, so distinctly obligatory for all other "sub-classes" of the Archaeocyathi. This radical change from a rigidly symmetrical to an entirely protean growth-form reminds Okulitch of a pathologic outburst of growing substance, completely irregular and lawless, like cancer growth in higher animals, and, like the latter, fatal to the parent organism, and even to the whole race, which suddenly became extinct sometime in middle or, possibly, early late Cambrian time. It is an alluring hypothesis that seemingly explains at one stroke both the peculiar asymmetrical encrustration and the cause of extinction of the whole class.

There seems no serious objection against a possibility that pathological growth in organisms is as old as life itself, even though John M. Clark strongly insists on the secondary nature and gradual development, mostly in post-Cambrian time, of "Organic dependence and disease" (1921). It seems even quite defensible philosophically to expect, as I do, a more nearly universal symbiosis of organisms in their earlier than in their later geological history, whenever conditions of life were crowded and an intense struggle for living space existed. Such were apparently the conditions of benthic life, which left evidence in the form of immense bio-topographic structures known as reefs; and it is known that Archaeocyathi are found in a great number of individuals in reef-like accumulations. It is also known that various sessile invertebrates (foraminifera, bryozoa, sponges), and plants (algae) incrust each other in a variety of complex combinations; such are occasionally mentioned by naturalists but perhaps as yet not studied in as much detail as they deserve. In such intimate symbiotic combinations it is sometimes not easy to draw a boundary between one and the other of its biologic components; some calcareous algae resemble encrusting foraminifera macroscopically and microstructurally so much that only a trained eye can distinguish one from another.

In view of this it seems that in the case of the fossil Exocyathi an assumption of their organic independence from the rigidly symmetrical cups of the Archaeocyathi, which they occasionally so completely encrust, would be more acceptable to most biologists than the hypothesis that they are immense pathologic outgrowths, a view which seems to suggest that asymmetrical and unruly Archaeocyathi were merely mutations or saltations (perhaps the macro-mutations of Goldschmidt) from an original symmetrical stock. Perhaps like a strangler fig that may occasionally strangle even one of its own kind, a strangler Exocyathus could have grown over some of its symmetrical and rigid relatives which provided it with a desirable support, and the latter could have been occasionally or even regularly strangled. On the other hand, the microstructure of the Exocyathi may be only "mimetic" of that of the Archaeocyatidae, and they could therefore belong to different kinds of organisms.

The Archaeocyathi are world-wide common Cambrian fossils which have been studied attentively only in the last fifteen years; there is apparently a great deal more to learn about them than has been revealed to date. Okulitch's monograph is well organized and scientifically balanced; the previous literature is covered exhaustively and critically; not only the morphology and anatomy, but also the ecology, ontogeny, and biological relationships of the fossil are described and discussed. Though most illustrations are attractive and clear, a few (photographs of *Mattewcyathus*) are illegible. Standardization of magnification might be recommended in the further studies, which, we may hope, will follow.

M. K. ELIAS

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OZARKIAN AND CANADIAN CEPHALOPODS. PART I: NAUTILICONES. PART II: BREVICONES. PART III: LONGICONES AND SUMMARY. *Geological Society of America Special Papers, Numbers 37, 49, and 58. By E. O. Ulrich, Aug. F. Foerste, A. K. Miller; with W. M. Furnish (I); with A. G. Unklesbay (III). The Geological Society of America, New York.* I, $2.00 (paper); II, $2.50 (paper); III, $2.50 (paper). I, x + 157 pp.; 57 plates. II, x + 240 pp.; 70 plates. III, x + 226 pp.; 68 plates. 1942; 1943; 1944.

Behind the somewhat dry monotony of the technical description of many genera and species of the earliest undoubted fossil cephalopods, there lies the important scientific and human drama of a one-man crusade for recognition, besides the universally accepted six, of two more Paleozoic geological systems: the Ozarkian and Canadian. Not since the "Sturm und Drang" days of the creation of modern geo-chronology, when the Cambrian, Silurian, Devonian, and Carboniferous periods of the Paleozoic were established, and to which somewhat later the Permian and Ordovician were added, has a more serious attempt been made at a revision of the whole concept of the Paleozoic era. With a patience and zeal seldom rivaled in the history of the geological sciences, E. O. Ulrich, with occasional help from associates and friends, has spent a good half of his lifetime in accumulating bit by bit geological and paleontological evidence indicating that between the two oldest Paleozoic systems, the Cambrian and the Ordovician, there are two other systems, fully equal to them in magnitude of time, and characterized by some marine organisms peculiar to them. In 1911 came a summation of geological evidence for the existence of the Ozarkian and Canadian periods, the ambitious "Revision of the Paleozoic Systems" published by the Geological Society of America; and in 1938 the same Society published the splendid monograph on the "Ozarkian and Canadian Brachiopoda," by Ulrich and G. Arthur Cooper. This publication broke through the sceptical resistance of Ch. Schuchert, himself a master in brachipod studies and Cooper's teacher, and convinced him of the existence of a Canadian period of time as a major chapter in the evolution of articulate brachiopods. Said Schuchert in his review (1939) of Ulrich and Cooper's brachiopod monograph: "On the basis of brachiopods, a good case can be made out for a Canadian system"..."with at least 31 genera..., of which 23 genera [are] restricted to this system."

In 1940 another of Ulrich's prominent opponents came out with this statement: "The establishment of the Ozarkian System as an independent system is the monumental achievement of Dr. Ulrich, and that he has triumphantly maintained it in spite of all opposition is a tribute to Ulrich's scientific acumen. As one of his former critics I take pleasure in acknowledging my conversion to his 'Ozarkian doctrine'" (Grabau, *The Rhythm of the Ages*, Peking, 1940). He also endorsed Ulrich's Canadian system.

Death claimed Ulrich on February 22, 1944, when the third and last volume of the *Ozarkian and Canadian Cephalopods* went to press. His close collaborator Foerste died in 1935, and A. K. Miller and his pupils and associates W. M. Furnish and A. G. Unklesbay shouldered the principal work of systematic description for the three volumes of the cephalopod monograph. The scope and importance of the work may be judged by the fact that the known number of species of Ozarkian and Canadian cephalopods of the world has been trebled: 287 new species are described and 126 previously known are revised, the whole being lucidly illustrated on 195 plates.

A reader who is accustomed to astonishing and bizarre forms from the far-away world of the geological past will be disappointed with the Ozarkian and Canadian cephalopods. Their shells, which are the only parts preserved as fossils, are simple septate tubes with little or no ornamentation. The cephalopods' great diversity of form, internal complexity, and fancy ornamentation came about much later in the Paleozoic and the Mesozoic. There are few features on which the classification of their early forms can be based: shape and size of conch, slight differences in septa, reflected externally in suture lines of the internal molds, and particularly structure of the siphuncle are the principal characters used in taxonomic distinction. By the combination of these are recognized species, genera, and families, which probably are not natural groups, but nevertheless permit orderly description of the fossil material. Equally arbitrary is their segregation into three major groups, the Brevicones, Longicones, and Nautilicones (a separate volume of description being devoted to each); but this grouping is practical and finds immediate justification in the chronological order of their appearance in the geological systems discussed.

The coiled Nautilicones appear in a great number of genera and species suddenly in the upper Canadian, as if the ability to coil originated as a mutation independently in several phyletic lines, or proved immediately so useful that coiled forms spread and evolved rapidly in the late Canadian seas; it seems that a combination of both causes was probably instrumental in their evolution.

Some of the numerous more or less curved Brevicones of the early Canadian apparently mutated into Nautilicones. The ability to curve slightly had been acquired already by the rare late Cambrian forms, as the earliest undoubted cephalopod *Plectronoceras* (originally described by Walcott, 1905, as *Cyrtoceras cambria*) indicates. The straight and curved Brevicones are taxonomically divisible into two major groups, "the Piloceratidae which is characterized by its large size and holochoantic siphuncle, and the Cyrtendoceratidae in which typically the conch is much smaller and the siphuncle is relatively slender and is orthochoantic in structure." The small Cyrtendoceratidae evolved into numerous forms in the course of Ozarkian time and reached their acme of development in the upper Ozarkian. Only a few Piloceratidae are known from the Ozarkian, mostly from its upper part, and they evolved into a sizable group only in the Canadian period. The long, slender, straight, and slightly curved Longicones are equally characteristic of the Ozarkian and Canadian and were cosmopolitan in distribution.

When reviewing *Ozarkian and Canadian Brachiopoda*, Schuchert pointed out the peculiar occurrence of by far the greatest number of species and genera of brachiopods in upper Ozarkian and upper Canadian times. The same is true for the Brevicones and Longicones, while Nautilicones were found exclusively in the upper Canadian. It seems too early to speculate on the cause of this fact: shells of both brachiopods and cephalopods of the Ozarkian and Canadian are comparatively so simple, and parallel evolution in their phyletic branches is so obvious (see Ulrich and Cooper, 1938) that restoration of the evolutionary sequence of their recognized genera is at the present time most difficult and has not been attempted for either the brachiopods or cephalopods.

Someone with stamina, patience, and enthusiasm equal to those of Ulrich should concentrate on the additional determined collection of a larger number of these fossils from their most prolific localities, in order to elucidate their evolution. Ulrich and his associates have done splendid pioneering in the establishment of an orderly succession of remains of invertebrates in the early Paleozoic rocks of America that justifies the validity of the Ozarkian and Canadian as major units of geological time.

It is a challenge to and an obligation of the new generation of geologists and paleontologists to do a better and more complete work on these rocks and their fossils.

M. K. Elias

GENETICS AND CYTOLOGY

The Dice of Destiny. *An Introduction to Human Heredity and Racial Variations.*

By David C. Rife. Long's College Book Company, Columbus, Ohio. $1.75. 163 pp. 1945.

Rife has written a simple and direct exposition of the nature of individual and racial human variations, leaving out of his account all such non-essential concepts as chromosomes and linkage. This unusual approach has avoided those genetic technicalities that appear so formidable to laymen.

The book begins with an explanation of the inheritance of simple human hereditary traits, such as the blood groups and tasting ability for phenyl-thio-carbamide, then takes up more complex characteristics, such as hair color, eye color, skin color, and stature; sex and associated traits; and, at some length, twins, dermatoglyphics, and handedness, subjects of Rife's own investigations. After a central chapter on the interaction of heredity and environment, the author considers mental capacity, special abilities, personality, and success or failure in life. Chapters on Race, and Genes and Democracy complete the discussion. Rife has for the most part expressed himself clearly and vigorously, in a way that will appeal to his readers. The book is sadly marred by numerous typographical errors.

There are certain lapses in precision of statement. For example, Rife begins his chapter on Heredity and Environment by saying, "The language one speaks is solely a matter of environment.... One's blood group is determined solely by heredity." These statements help to perpetuate in popular thought that very dichotomy between heredity and environment Rife himself clearly wishes to avoid. After all, the capacity to learn and speak a language—any language at all—is genetically determined, and the first statement therefore cannot be strictly true. And there have already been many instances, such as that which Rife points out elsewhere of diabetes mellitus (in error confused with diabetes insipidus in the text), where "solely hereditary traits" have become through discovery shifted to the class of the environmentally controllable. The real point is that no phenotypic trait develops except in an environment of some sort, and that therefore all are potentially modifiable, even if only in a lethal direction. These criticisms would be unfair of a book with the aim of this one, were it not that general understanding of the real nature of the relation of heredity and environment is so fundamental and so widely misunderstood. Rife has himself said in another passage:

> If a trait is shown to be hereditary, the attitude all too frequently is that nothing can be done about it. Conversely, if a trait can be altered by environment, it is usually assumed that heredity has nothing to do with it.

Yet he has himself perhaps contributed to further misunderstanding in this regard, from his very choice of title. *The Dice of Destiny* is a striking phrase that will leave many a reader, I am afraid, with a sense of the irrevocable and irremediable nature of heredity, in spite of all the author's cautioning.

With the author's views on eugenics most geneticists are likely to concur, although some will question the advisability of a general sterilization of morons, for which he argues. With his views on race more will differ. There are several controversial issues here. One arises from the statement that "the genetic differences between human races are similar to those between breeds of animals." This is true and not true—true if referred simply to the fact that differences in gene frequencies exist in both; not true in the sense in which so many will unfortunately take it, that human races are as dissimilar as the breeds of animals that are the product of artificial selection. Rife, of course, recognizes the action of natural selection in the one case and of artificial selection in the other, but he does not apparently consider the vast differences, both quantitative and qualitative, in their effects. One aspect of this question has already been more than adequately discussed by Dobzhansky in another review of this book (*Science* 102: 234. 1945). The argument that "because psychic traits in animals are rather rigidly determined by heredity they are so determined in man" seems indeed weak if natural selection in man has worked steadily for the most adaptable and modifiable type of genetic determination of intelligence and personality, while in other species it has not.

Another ground for differing with the author lies in the reasoning that because the genetic basis of racial and individual differences is the same, therefore "evidence of genetically determined mental differences must of necessity be considered evidence of similar differences between racial groups." It does not necessarily follow that because blood groups are inherited, the frequencies of the blood groups are different in different races. It happens to be true, but it had to be separately demonstrated. No matter how probable it may be that races differ in the frequencies of specific genes affecting mental differences, it remains to be proved that they do so differ, and further that, even if they differ, such differences are not offset in effect by complementary differences. There are many well established cases where even different species possess the same or very similar phenotypic traits that depend upon quite diverse genetic bases.

Finally, the view that "the greater the heterogeneity of a population the greater are the difficulties in attaining and maintaining democracy" is certainly questionable unless carefully qualified. It can be equally well maintained that, up to a point, civilization, and with it democracy, depend upon human diversity and non-homogeneity. Certainly such a view as that quoted above has no scientific validity, and its statement by a scientist as simple fact rather than as personal opinion may be vastly misleading.

Perhaps the best recommendation of this book is that it arouses such discussion. There is no doubt whatever that after the extreme views that have been expressed in recent years as to the absence of genetic racial differences in man, a book of a more conservative standpoint, such as this, has been sorely needed.

BENTLEY GLASS

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A STUDY OF SPONTANEOUS MUTATION. *University of California Publications in Zoology, Volume 49, Number 10.*

By Richard B. Goldschmidt, with the collaboration of Richard Blanc, Werner Braun, Mary M. Eakin, Ruth Fields, Aloha Hannah, Leonie Kellen, Masuo Kodani, and Claude Villee. University of California Press, Berkeley and Los Angeles. $3.00 (paper). Pp. 291–550; plates 23–30. 1945.

This is the long awaited detailed report of data on mass mutation to which Goldschmidt has referred in shorter communications over a period of years. Consisting of some 125,000 words with 153 tables, many of them full page, and 98 figures of wing mutants and salivary chromosomes in both text and in additional plates, it is matched in extent only by the tremendous volume of work done by the senior author and his collaborators.

A careful reading of any part requires constant reference to the tables and a check of the material presented in other sections. Few readers will have either the time or the patience to read the entire treatise. The reader with little time at his disposal may get the gist of the facts presented, and of Goldschmidt's interpretation of these facts, by reading carefully the introduction, pp. 291–292, and the discussion and summary, pp. 524–530.

The bulk of the paper may be divided into a section dealing with spontaneous mutation, largely in a stock of plexus flies (pp. 293–297 and pp. 471–524), and a section dealing with the details of phenotypic expression of certain multiple allelic series mainly at the silver, arc, and plexus loci, factor interaction, modifiers, and chromosome aberrations affecting this expression. The first of these sections presents the details which most geneticists interested in spontaneous mutation will want to study.

There seems little doubt from the facts reported here that the plexus stock has shown a uniquely high mutation rate at the silver, arc, and plexus loci, these mutations being in the form of a complex allelic series at each locus, and consisting in some cases of reverse mutation to or toward the so-called wild-type. Furthermore, these and a few other loci, including rudimentary, have mutated in a non-random manner, so that several mutations appeared either simultaneously in a pair mating or in the course of a few generations in a carefully pedigreed line. No explanation in terms of contamination or by mutation of a single suppressor having action at several loci can explain the facts. It is true that a valid scheme which spreads the occurrence of the mutations over a somewhat longer series of generations that Goldschmidt has postulated can be presented. But this in no way invalidates the main argument for the high mutation frequency at the several loci involved and for the non-random distribution of these mutations in time and in certain lines. In general, these findings are in line with recent work on high spontaneous mutation frequency in certain lines and particularly at specific loci, as reported by several investigators (Berg, Demerec, Neel and Spencer). It is also shown that the plexus line and its derivatives produce frequent small chromosome aberrations in the form of deficiencies, principally in the X-chromosome, and corresponding translocations to the 2nd and 3rd chromosomes. While these deficiencies and translocations seem in some cases to have arisen at or near the same time as the mutant alleles at mutating loci, they do not cover these loci. However, their presence in conjunction with the mutants results in peculiar ratios, particularly of sex-linked mutants in certain out-cross and back-cross tests.

Goldschmidt interprets these findings to mean that the mutation process is one dealing with the mechanical breakage of chromosomes, sometimes breakage on an intra-salivary band scale, in contrast to an interpretation of point mutations as chemical changes in genes. It should be stated that the mutants in question can be dissociated from the chromosome aberrations by crossing-over and then behave as typical point mutations. It would seem that the demonstration that certain cases of deficiency are of intra-band magnitude would leave the ultimate answer on the nature of point mutation to a time when analysis at a new level can be achieved.

The section on factor interaction and phenotypic expression presents in great detail a study of the several alleles, in heterozygous and homozygous form, at the silver and arc loci, the interaction of these compounds at the two loci, and epistatic effects when in combination with other mutants, particularly plexus. As both allelic series are extensive and both act on wing shape, it is not surprising that a complex array of phenotypes has been produced. Certain of these compounds and permutations are extremely susceptible to modifier action and therefore serve as excellent tools for testing for the presence of genetic variability in out-crosses to various wild-type and mutant stocks. Often the phenotypic expression is non-predictable in simple additive terms. Perhaps the chief value of this work has been the discovery of a background of genetic variability which would have gone undetected in the absence of the sensitive markers used. The work would have added value had it been done under carefully controlled environmental conditions and had these been specifically stated. Temperature, moisture, food medium, condition for pupation, larval crowding, etc. have marked effects on the phenotype of such genetic combinations as are here described. Without control of these factors, the carefully recorded results in this long series of experiments could in many cases not be duplicated upon repetition. It is not unlikely that some of the unexplained variability in results in certain experiments is due to environmental as well as genetic variability. However, much of interest concerning factor interaction is amply demonstrated.

As Goldschmidt has published elsewhere and here repeats an explanation of Demerec's miniature case in *Drosophila virilis* as being due to factor interaction rather than to a frequently mutating gene, it is only fair to state that a careful reading of Demerec's papers on frequently mutating genes reveals that he has made the critical tests demanded by his hypothesis and that the factor interaction explanation is invalid.

Typographical errors, particularly in the tables, some contradictory statements, and the confusing use of the symbol for a mutant when the stock containing the mutant is really meant, add to the difficulty in reading this section.

In conclusion, it may be stated that the phenomenon of repeated and non-random mutation in a particular stock has been well demonstrated; the data add considerably to our knowledge of the mutation process; and the results could only have been secured by the laborious method of rearing over a period of years long inbred lines carried on by pair matings. No other student of *Drosophila* genetics has as yet carried out this type of experiment on so large a scale.

WARREN P. SPENCER

CONSTITUTION AND DISEASE—*Applied Constitutional Pathology. Second Edition.*

By Julius Bauer. Grune and Stratton, New York. $4.00. xiii + 247 pp. 1945.

In *To Begin With*, Raymond Pearl attempted to provide for young biologists a selection of essential reading. Among the books he included in his list was one by

Julius Bauer, *Die konstitutionelle Disposition zu inneren Krankheiten*, in order, he said, "that it may become even clearer that genetics has relation to medicine." Were this list to be revised today, the book here reviewed might well replace that earlier discussion of the same subject. Readers in this country should be expecially grateful for an English version.

Constitution and Disease is a briefer book than the original, but remains comprehensive in its consideration of the relations of genotype to disease. Its survey of the literature, up through 1944, is remarkably thorough. In an introduction, Bauer deals with the meaning of normality and abnormality, the causes of variability, and the insight into the significance of constitution in relation to disease afforded by the study of identical twins. The author proceeds to define "constitution" as the realization in the phenotype of the potentialities of the genotype, and discusses with abundant examples the significance of constitutional factors (read "genes") in the etiology of diseases, in the alteration of the clinical pictures and courses of diseases, and in necessitating modifications in treatment. Next Bauer considers the constitutional inferiority centered in certain organs or tissues such as nervous system, heart and blood vessels, and digestive tract. Racial differences offer further evidence of the widespread existence of differences in the superior or inferior general resistance to disease of specific organs or tissues. Two chapters deal especially with the integrative systems of the individual constitution, the endocrine and the nervous. In the former the relation of genotype to endocrine glands, and to ultimate characters either through the endocrines or directly, is particularly lucid. The treatment of the relation of the genotype, nervous system, and ultimate expression of characters shows that Bauer was a leader in psychosomatic medicine long before the coinage of that term made its concepts popular among medical men. The classification of normal and abnormal constitution is characteristic of the author's thought. While agreeing that many of the earlier classifications of constitution were over-refined, he believes there is sound evidence for the existence of certain endocrine types, certain neuropathic constitutions, an asthenic constitution, and various diatheses of significance. Besides these, he describes a "status degenerativus," which appears to be no simple nor readily defined constitutional type, but simply a consequence of the chance inheritance by a single individual of a number of detrimental genetic traits. In this respect it is to be contrasted on the one hand with the pleiotropic effects of a single gene, and on the other with the consequences of linkage in heredity.

A chapter on certain major diseases with chiefly constitutional etiology serves to illustrate the principles previously considered. Diabetes mellitus, obesity, essential hypertension, various anemias, leukemia, Hodgkin's disease, hemophilia, peptic ulcer, and cancer are among the conditions considered here. A final chapter emphasizes the importance in the "ars medica" of modifying treatment to fit the individual patient, due regard being had for his particular constitution. One passage should be taken to heart by all doctors:

> "Sometimes the following objections can be heard: There is no difference in the treatment of obesity, whether or not its constitutional (hereditary) character is recognized, therefore it is unimportant to be familiar with the latter; the same should be true with regard to other hereditary diseases. The correct aspect of the matter, however, is different. The physician carrying out a treatment must know as much as possible about the etiology, pathogenesis, and consequences of a pathologic state that he is about to treat. Otherwise he deserves the title of quack rather than of doctor."

Space fails for the adequate discussion of this truly important book. It is, to be sure, not without its faults. Only a medical man will be able to read it without a medical dictionary at hand for frequent consultation. The style is heavy and didactic. Bauer often assumes far more fundamental understanding of genetics than most of his medical readers are likely to have. He often cites evidence without discussing it thoroughly. Consequently he will impress many as dogmatic and arbitrary in his opinions. This is the more to be deplored because such a book as this is greatly needed and should have the widest possible influence. In any case, let it be required reading for every geneticist and every medical student.

Bentley Glass

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Heredity in Dairy Cattle. *Lessons in Breeding and Herd Development for 4H and FFA Dairy Clubs and Other Beginners.*

By James E. Russell. The American Guernsey Cattle Club, Peterborough, New Hampshire. $2.50 (free to 4H and Future Farmers of America members). xvi + 135 pp. 1944.

Written for the practical farmer at the most elementary level, this book should serve as a useful guide for the improvement of animal stock.

Russell addresses himself specifically to "4H and FFA Dairy Clubs and other beginners." He includes a brief and very general discussion of the theory of genetics; and while, this might be enhanced by some good diagrams of chromosome behavior, it must be conceded that he effectively makes the points he wants to make. References to text-books for further study of genetics are added. The main part of the book teaches by example, describing in detail four successful Guernsey herds and the procedure by which their owners built them up, and drawing practical conclusions from these "case histories."

Eileen Sutton Gersh

THE ARTIFICIAL INSEMINATION OF FARM ANIMALS. *Edited by Enos J. Perry. Rutgers University Press, New Brunswick, New Jersey.* $3.50. 265 pp. 1945.

Another book for the practical farmer, this one deals with more advanced theory and practice. Chapters are devoted to detailed accounts of the reproductive system and principles of genetics (Mendelian laws, linkage, sex linkage, multiple factors, lethals). Here again a diagram of meiosis might be helpful, and in addition it would be well to stress the statistical nature of genetic ratios, instead of leaving the impression that they correspond exactly with actual results.

Besides chapters on such topics as breeding systems, selection of animals, general technique of insemination, control of disease, and the organization of breeding associations, there are special chapters by experts on the application of artificial insemination methods to cattle, sheep, horses, birds, and swine.

EILEEN SUTTON GERSH

GENERAL AND SYSTEMATIC BOTANY

SARGENTIA. V. FRAGMENTA PAPUANA (*Observations of a Naturalist in Netherlands New Guinea*). *By H. J. Lam. Translated by Lily M. Perry. The Arnold Arboretum of Harvard University, Jamaica Plain, Massachusetts.* $3.00 (paper). iv + 196 pp. 1945.

The author of *Fragmenta Papuana* is at present Director of the Rijksherbarium at Leiden, but in 1920–1921 he was botanist to the Van Overeem Mamberamo Expedition into the high mountains of Netherlands, New Guinea. Between 1927 and 1929 he published, in the Dutch language, a series of seven articles describing his experiences with this expedition, all of them in Natuurk. Tijdschr. Nederl.-Ind. In the course of her studies of the New Guinea collections made by L. J. Brass in the 1930's, Lily M. Perry soon realized the significance of Lam's papers for anyone dealing with the plant life of the interior of that little-known region. It is due to her initiative and industry that we now have excellent English translations of Lam's seven papers.

The *Fragmenta* comprise a sort of botanical journal of the Mamberamo Expedition. Lam's material collections, in the form of specimens and records, are of course extensive; but like all trained field men, he found himself with a wealth of general information about the vegetation of the country for which there was no place in his formal records. He gives us these observations in the *Fragmenta Papuana*, interspersed with accounts of travel, climate, animal life, and the native aboriginal population.

The first of the seven articles is introductory. It contains a brief history of the exploration of the Mamberamo River, an account of the personnel and itinerary of the expedition of 1920–1921, and a description of some further explorations in 1922. The second article is very short, and is devoted entirely to meteorological observations made on the journey.

Fragments 3 to 6 inclusive deal with sections of the journey which fall within an equivalent number of phytogeographic provinces. Number 3 contains "Impressions of the Lower Mamberamo Territory"; number 4, of "The Meervlakte and the foothills"; number 5, of "The north slope of the Central Mountain Range"; and number 6, of the country "Above the forest limits: Doormantop and its vegetation," The seventh Fragment records the author's personal observations upon the "Land and people of the Dika and Toli Valleys." In each section there are notes on travelling conditions, with personal impressions of landscapes and vegetation, often supported by pen and ink sketches. Of particular interest and significance are the author's descriptions of plant communities, habitats, and growth forms.

It is difficult to designate outstanding features of Lam's papers, for together they make a connected story in which the standard of excellence remains high. I venture, however, to point out some features that seem worthy of particular note. The botanical descriptions of landscapes are extraordinarily effective and clear. The author obviously is cognizant of the complex methods now commonly used by ecologists for describing plant communities; yet he adheres to "plain language," and achieves living descriptions that can without a glossary be read and understood by anyone. A second fetaure of unusual interest is in Fragment 6 (pp. 123–137 of the translation). Here are observations on the ecological adaptations of alpine plants in New Guinea, with a discussion of theories for their origin and development. Here also is a general consideration of the origin and affinities of the New Guinea flora. The descriptions of the strange peoples met with in the high mountain valleys (Frag. 6) make a rather thrilling final chapter. The explorers found themselves literally in a stone-age civilization, for the people had tools made only of stone, bone, or wood. Curiously enough, they turned out to be friendly beings, living in agricultural communities on high slopes that required to be terraced for cultivation. Their contacts with the outside world had been almost non-existent, but there is some evidence that they had a tenuous connection with lowland races. Lam presents interesting botanical evidence of the extent and nature of this connection.

The *Fragmenta* make splendid reading not only for the professional botanist, but for the vicarious general traveller as well. Some of the botanical descriptions are much too detailed for anyone who has not had personal experience with tropical floras, but these paragraphs can be skipped without loss to the structure as a whole. The papers could have been made somewhat more acceptable to the general reader if the author had segregated his annotations on plants and growth habits in such a way as to make them instantly recognizable as such.

Lily M. Perry is to be congratulated upon the excellence of her translation. She has followed the Dutch text very closely, and has so arranged the legends for the text figures (reproduced directly from Lam) as to make them clear to readers of English. Lam's text references to his collection numbers and his citations of literature are retained throughout. The index to the translation is partially annotated by subdivision under various subject headings.

H. M. Raup

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The Structure and Reproduction of the Algae. *Volume II. Foreword, Phaeophyceae, Rhodophyceae, Myxophyceae.*

By F. E. Fritsch. Cambridge, at the University Press; New York, The Macmillan Company. $12.00. xiv + 939 pp.; 2 maps. 1945.

That in England between the years 1935 to 1945 a manuscript of such magnitude and complexity could be so thoughtfully, accurately, and successfully prepared, that it should be so well edited, printed, proofread, and put together is nothing short of miraculous and reflects the highest possible praise upon its author, its editor, and the Cambridge University Press.

This second volume of Fritsch's monumental account of the primarily marine algae proves a fitting companion to the earlier one, in which an exhaustive account of the predominantly fresh-water forms was given. In format, it follows closely the first volume that, in turn, was patterned after Oltmann's classic *Morphologie und Biologie der Algen.*

After a Preface which outlines the scope of the volume and includes acknowledgments, there follows a Foreword. Here are found generalizations on the conditions of life, distribution, and special ecological characteristics of the habitats frequented by these algae. There is then included a discussion of the seasonal occurrence and geographical distribution of the marine forms. The latter account is supplemented by two most interesting maps, found in an appendix (not in the body of the text, as stated) in which are shown the geographical distribution throughout the world of certain seaweeds. The effects of differences in temperature, light, salinity, etc., on distribution are discussed, and striking instances of discontinuous ranges of species and possible endemism are cited. The general conclusion with respect to endemism is that ". . . our knowledge of distribution of marine Algae is still too limited to provide much positive evidence as to the existence of endemic genera and species."

The body of the text follows in the main the outline of the companion volume. Each of the classes is discussed primarily from a morphological and developmental standpoint, only the principal outlines of the taxonomy being considered. Such features as the vegetative construction, cell wall, chromatophores, special morphological features, cytology, and life cycles are described in great detail; and the whole is copiously and accurately documented throughout.

After the account of each class and order, there is a comprehensive list of literature to which reference has been made in that portion of the text. For so complex a work, this system of recurrent bibliographies no doubt facilitates locating a particular citation in the text and certainly has the sanction of the parent work *Morphologie und Biologie der Algen.* It does result, however, in lending a certain discontinuity to the volume as a whole, and some repetition—insignificant criticisms if in their present position the citations are more useful to the reader.

The figures, of which there are more than 2,000, are chosen to illustrate morphological features described in the text. These are taken from various authors and, considering the grade of paper available in these times, have been reproduced fairly well. Some, however, have suffered from too much reduction but are, nevertheless, informative.

Throughout the volume interesting material on the biology of the various forms is given. This is particularly well done in the Myxophyceae where, in a section on distribution, ecology, and biology, extensive information is given concerning the unusual habitats in which these algae are found. These include such diverse situations as thermal springs, frigid lakes of the Antarctic, the surface of black sulfide muds on solar salt works, inside the human mouth, etc. Their activities as lime-borers and lime-depositing agencies, as well as their better known role as symbionts associated with fungi ("lichens"), bryophytes, gymnosperms, and Protophyta are also discussed.

The volume closes with an index of authors cited in the text, bibliographical references being distinguished by boldface page numbers from those in the body of the text, and an index of contents some thirty pages in length. As previously mentioned, two maps are tipped in at the end.

Naturally, it is impossible for one unfamiliar with the field of algology to evaluate the contents. However, from the clear and concise language in which it is written, the skillful manner in which the material is organized, the reputation of the author as an algologist, one instinctively realizes that here is a classic which will be of inestimable aid to future generations of students of these most interesting organisms.

F. K. Sparrow

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A Manual of Soil Fungi.

By Joseph C. Gilman. The Collegiate Press, Inc., Ames, Iowa. $5.00. xi + 392 pp. 1945.

As stated in the preface, the present volume is an outgrowth of an earlier paper by E. V. Abbott and J. C. Gilman entitled "A Summary of the Soil Fungi." Because of the continuing demand for this paper by soil microbiologists, industrial mycologists, and medical workers, the junior author felt an up-to-date revision highly desirable.

The volume is, admittedly, a compilation of descriptions of soil fungi and "...is designed to place a tool in the hands of investigators that will enable them to identify the soil fungi..." For the most part the arrangement followed is that of Lindau in Engler & Prantl, *Die natürlichen Pflanzenfamilien*. The Phycomycetes and the large genera *Penicillium*, *Aspergillus*, and *Fusarium* follow the treatments of modern specialists. Agarics, soil-borne plant pathogens not yet reported directly from the soil, those in leafmold, decayed wood, or other materials not yet fully incorporated into the soil are excluded, as are the Actinomycetes and the carnivorous Zoopagaceae.

Following the preface there is an introduction, consisting of brief discussions of the functions of the soil, the role played by fungi in the biology of the soil, and their further role as airborne entities that may become serious factors in the contamination and subsequent deterioration of commercial materials. There then follow brief sections dealing with the nature of fungi, as well as their sexual and asexual methods of reproduction, and finally concluding with an analytical key to the classes, orders, and families of the fungi to be considered.

For each of the classes, orders, families, genera, and species there is a technical diagnosis and, where necessary, keys to the genera and species are supplied. Authorities are given, without citations, for genera and species. The principal synonyms of the species are included and, following the specific description itself, the countries in which the fungus has been recorded, together with references to pertinent papers. A noteworthy feature of the 133-page section on Phycomycetes is the 76-page treatment of soil-inhabiting Chytridiales, Blastocladiales, Monoblepharidales, and Saprolegniales, groups ordinarily omitted in most books on soil microbiology. Descriptions of the terricolous Ascomycetes occupy 20 pages; the Fungi Imperfecti, including forms with ascogenous stages, 192 pages; and the Mycelia Sterilia, two pages. There then follows a bibliography of 169 titles, a six-page glossary, and an index to the genera and species.

A highly valuable feature of the manual is that each generic description is accompanied by a small block figure illustrating the principal features of the genus. The utility of these drawings is marred in a few instances, however, by inaccurate copying and at least one error in identity. Thus, in Figure 16, from Ward, illustrating a chytrid, *Rhizophlyctis rosea*, the zoospores are shown emerging from a sporangium which, in the original paper, was immature. Figure 17, from Whiffen, of a polycentric chytrid, *Nowakowskiella*, is here shorn of one sporangium and is devoid of an operculum, important diagnostic features present in the original. Figures 19a and b, intended to illustrate the genus *Blastocladiella*, are in reality figures of *Blastocladia parva*.

The book will beyond question prove highly useful to the general soil microbiologist and others, as has been evidenced by the popularity of its shorter predecessor.

F. K. SPARROW

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CATALOGUE OF THE VASCULAR PLANTS OF S. TOMÉ (*with Principe and Annobon*).

By Arthur Wallis Exell, and other members of the Department. The British Museum (Natural History). £1 10s. xi + 428 pp. 1944.

The vascular flora of three volcanic islands in the Gulf of Guinea is the subject of this paper recently published by the British Museum. Exell collected personally on S. Tomé, Principe, and Annobon in 1932 and 1933, visiting also the island of Fernando Po. In addition to his own collections, he examined most of the earlier plant records from the islands, specimens for which he saw in European herbaria. Thus the work achieves that degree of definitiveness that is possible only when a floristic student has access to original collections and types.

Most of the book is devoted to the critical catalogue of the flora, wherein there are the necessary synonymy, citation of specimens, geographical and ecological notes, and discussions of imperfectly known species. The text for a few of the families was prepared by specialists, but most were done by Exell himself. Totals of 36 new species and 4 new varieties are described, many of them illustrated by line drawings. In addition 35 new names or new combinations are proposed.

Some 55 pages at the beginning of the book are devoted to two chapters dealing first with the geography and geology of the islands, a short history of their botanical exploration, and descriptions of the general aspect of their vegetation. Second, there is a review of the phytogeographic origins and affinities of the flora. The islands prove to have a prevailing floristic relationship with the neighboring coasts of Africa, but they demonstrate also the effects of insular isolation and endemism. Endemics on one or more of the three islands total 171 among the 683 species regarded by the author as geographically significant. He finds that "each island has (in addition to its endemic species) a comparatively large number of species found on the mainland but not on the other islands," and concludes that "this, again, seems strong evidence that the islands were never connected with each other, but that each received an independent quota from the rich mainland flora." In the second chapter (pp. 48–49), there is a critical analysis of the sources of error that commonly rise when floras are compared statistically. This analysis could be studied with profit by anyone whose phytogeographic problems involve such comparisons.

Although the work is devoted primarily to the vascular flora, a list of the non-vascular cryptogams collected on Exell's expedition of 1932–33 is included as Appendix I. A second appendix gives a list of vernacular plant names used on the islands.

H. M. Raup

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The Orchids of New South Wales.

By H. M. R. Rupp. National Herbarium, Sydney, N. S. W. 9s. (cloth); 6s. (paper). xv + 152 pp. 1943.

This book was issued by the National Herbarium at Sydney as a part of a projected "Flora of New South Wales." It contains descriptions of 252 species, representing 40 genera. In a few cases, varietal distinctions are made within the species. The paper is amply supplied with keys. Rather detailed descriptions are given for each species, and there are 23 plates containing excellent line drawings. Two new varieties are described by the author in the main part of the text. One is *Dendrobium Kestevenii* var. *coloratum*, and the other is *D. Kingianum* var. *pulcherrimum*. In an addendum, however, descriptions of five new species of *Diuris* are given. These were contributed by Mrs. Pearl R. Messmer and are as follows: *D. semilunulata*, *D. victoriensis*, *D. polymorpha*, *D. flavopurpurea*, and *D. lineata*.

For each species is given the date of the original publication and the principal synonymy. Wherever common names are available they are also included. The geographical distribution is first summarized, and then supported by the citation of specimens. In the summarized distribution four main divisions of New South Wales are used. These are based upon the major topographic provinces: coastal, tableland, western slopes, and western plains areas. They are looked upon as natural divisions, whose growing conditions reflect differences of climate. No map of these provinces is included, but the student is referred to a paper by Anderson on "Trees of New South Wales" (1932), where such a map is published. The book closes with an explanation of specific and varietal names, a general glossary of botanical terms commonly used in the paper, and an index to species and varieties which contains also author citations.

The introduction to the book deserves some special attention. It does much to make the book useful to the amateur botanist, whereas the professional taxonomist would be content with the bare taxonomic and geographic treatment. The author gives a well written and clear description, illustrated by sketches, of the principal parts of an orchid flower, followed by a brief discussion of other characteristic features of orchid life. The history of orchidology in New South Wales is adequately summarized. Advice is given on methods of collecting, in a brief section which contains also some very interesting and significant notes on local distribution and habitat selection among the orchids. These notes might well have been enlarged upon and made into a very useful addition to the whole discussion. It is obvious that the author speaks from wide experience in the field, and, as is so often the case among floristic students, the common facts about places in which plants live are either passed over as of little importance, or are considered to be of such general knowledge as to be unworthy of mention.

H. M. Raup

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Flowers in Britain *Wild, Ornamental and Economic and Some Relatives in Other Lands.*

By L. J. F. Brimble. Macmillan and Company, London. $4.50. x + 393 pp.; 18 colored plates. 1944.

Flowers in Britain is a non-technical book concerned with wild and garden flowers and economic plants of the British Isles. In the words of the preface, the book is "written for anyone who is interested in or wants to know something about flowering plants. It is not intended solely for the professional botanist, and therefore no previous knowledge of botany is assumed."

It is impossible for an American who is unfamiliar with the British landscape to examine critically the actual floristic content of the work. The method of presentation, however, is intriguing and worthy of comment. Floristic books, particularly in America, usually run to one or the other of two extremes. They are either as dry as the specimens which the conscientious botanist studies before he prepares the skeletonized and uninspiring, although technically correct work; or they are reduced to poetic or insipid descriptions of the beauties of Nature. Somewhere in between these extremes there ought to be a golden mean, and Brimble gives evidence of having come close to it.

The book begins with three introductory chapters which tell the reader what a flowering plant is and give a general survey of the significance of flowering plants in the development of modern civilization. Then comes a chapter on flowers: how they are made, how they vary, and how they function. In the preface the author has already placed high in the list of basic requirements for the beginning botanist that he learn to see how plants differ from one another, how they are related, and what their names are. The third chapter enlarges a little upon the idea of classification and explains how it has come about. Here the author explains in a few simple sentences how he has organized the material of the book and why. The remainder of the text is arranged in chapters dealing with single families or small groups of families of flowering plants. The order of treatment is taken from Hutchinson's *Families of Flowering Plants*, and begins with the buttercups.

Within the treatment of each family are three subdivisions: first is a description of the wild species; second, a brief treatment of the species of the family which are commonly cultivated as ornamentals in English gardens; and third, some account of the economically valuable plants which come from the family. All this is done in simple but delightful English. There are no keys, but a few descriptive phrases are usually slipped in to make possible the separation of common species within the genus. Common names are given in boldface type, with Latin names italicized and in parentheses. For identification the author further relies upon habitat notes, and upon habit photographs and colored plates. There are 17 of the latter, each consisting of several colored drawings and inserted in its appropriate place in the text. The pictures are small, but nonetheless effective for the recognition of common plants.

The book is delightfully readable, and numerous bits of verse scattered through it are selected with unusual perspicacity. Not the least of the attractions are the short descriptions of plants useful to man. In them the author has tapped a seemingly inexhaustible well of human interest—one that is apparently unknown to most authors of floras, popular or otherwise.

I hope the author will not be offended if we in America find a little amusement in what he says about Indian corn. Having had some experience with British ideas about corn, I turned eagerly to see what Brimble would have to say on the subject. On page 375 is the following gem:

"**Maize** or **Indian corn** (*Zea mays*) is now cultivated throughout tropical and sub-tropical regions, though it is also grown in certain temperate areas. It is a native of Mexico. It is indeed a useful plant for the grain is converted into flour by grinding, it is also eaten without grinding, and in this form when dry fed to poultry; the green cob is a very favourite vegetable; the leaves are used as fodder; the spathes surrounding the unopened spikes are used in papermaking; and the dry cobs are used for firing."

Not a word about the Missouri Meerschaum!

H. M. RAUP

A BOOK OF WAYSIDE FRUITS.

By Margaret McKenny and Edith F. Johnston. The Macmillan Company, New York. $2.50. 78 pp. 1945.

In this unusually attractive little book the author and her artist have chosen for description and illustration about 33 varieties of familiar and beautiful fruiting plants commonly seen along the wayside in early summer, midsummer, and autumn. The brief description of each plant included in the text is accompanied by a full-page color plate, very well executed, and illustrating not only the fruit but the flowers and foliage as well. Those who are familiar with the companion volumes on garden flowers and wild flowers previously published by the author and the artist will welcome this new addition.

POISONOUS PLANTS OF HAWAII.

By Harry L. Arnold. Tongg Publishing Company, Honolulu, Hawaii. $2.00. 71 pp. 1944.

This little book, although it contains but two chapters and covers only 71 pages, apparently deals rather thoroughly with the poisonous plants of Hawaii. In the first chapter attention is given to the common and truly dangerous plants, of which there are less than a dozen. The habitats, common names, and recognition characters are given for each species, together with its poisonous principles, the symptoms of poisoning from them, and antidotes with which to combat the effects. The second chapter is devoted to a comprehensive plant list in which are described "all of the plants which have been listed by various authors as being poisonous, followed by as accurate information as is available regarding their distribution and their poisonous nature." Some of these have proved non-toxic, while others are either uncertainly or only slightly poisonous, or so rare as to make them of no great significance. The book closes with a bibliography of 48 titles and an index to both common and scientific names.

There are 24 plates containing excellent line drawings, all of them reproduced from Otto Degener's *Flora Hawaiiensis*. The author also credits Degener with the solution of intricate problems of taxonomy and nomenclature involved in the work.

The book is clear and in general well written. One is impressed with the small number of plants in Hawaii which are actually dangerous to man or his domestic animals. They are all apparently easily recognizable, and this book should do a great deal to make them of common knowledge and thus to reduce the number of cases of poisoning.

H. M. RAUP

ECONOMIC BOTANY

THE ENCYCLOPEDIA OF FRUITS, BERRIES, AND NUTS AND HOW TO GROW THEM.

By Albert E. Wilkinson. The New Home Library, The Blakiston Company, Philadelphia. 69 cents. ix + 271 pp. 1945.

This small volume, scarcely comprehensive enough to be called an encyclopedia, is divided into two parts. The first treats in alphabetical order the familiar as well as many of the exotic fruits, berries, and nuts which are grown in the United States and other parts of America. The largest amount of space is devoted to the more important crops, such as apples, peaches, plums, strawberries, and the like. These are discussed in detail from the standpoint of description, types, varieties, soil, climatic requirements, planting, cultivation, fertilizing, pruning, insects, diseases, and propagation. Common or botanical names by which fruits, berries, or nuts are known are listed alphabetically with cross-references to the name, usually a common name, under which the descriptive material is found. Some of the botanical names, unfortunately, are not correct.

The second part of the volume is a gardener's guide which brings together general instructions and suggestions applying to the fruit garden as a whole. Recommendations of varieties and planting arrangements are given for various regions of the United States in considerable detail.

The book is obviously intended for the small home gardener whose botanical and horticultural knowledge is limited. For this purpose it should prove useful.

P. C. MANGELSDORF

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GREEN CARGOES.

By Anne Dorrance. Doubleday, Doran and Company, Garden City, New York. $2.00. 187 pp. 1945.

Reading in this book about the transport of seeds and plants about the world, from the time of the Phoenicians to the present day, has a great deal in common with walking through a rambling old garden with a guide. Here is a peach trained on the wall, here are fragrant lavender and allspice, here a stalwart row of tulips. Some of the plants are native Americans; others have become "naturalized," and we hear of their origins and the sometimes hazardous voyages which brought them to different parts of the world. Not that the book is confined to garden plants—economic crops such as rubber, quinine, and cereals are also considered.

The profusion of interesting stories makes this an entertaining little book, though its usefulness in other respects is limited, the more so by the absence of any index of plant names.

EILEEN SUTTON GERSH

GENERAL AND SYSTEMATIC ZOOLOGY

THE MARINE ANNELIDS OF NORTH CAROLINA. *Duke University Marine Station, Bulletin No. 2.*

By Olga Hartmann. Duke University Press, Durham, North Carolina. $1.00 (paper). 54 pp. 1945.

This clearly printed, clearly illustrated little volume promises to be so useful that it will be a "must" for anyone seriously interested in any kind of work ininvolving any of the marine annelids of our Atlantic coast. Because it is close to Cape Hatteras, Beaufort, where this study was made, claims most, though not quite all, of the annelids found from Maine to Florida.

Each species is described briefly and many are illustrated in the ten full-page plates of line drawings. Synonyms, bibliography, distribution, and ecology are given with special notes about habitat, abundance, breeding habits, and salient features for tentative identification in the field. Under each family there is a key to the species. The list of ecological associations and habitats gives the species to be found in each. The usefulness of the book is further enhanced by a list of characteristic trails, surface marks, and tubes; an index; a bibliography; and maps of the Beaufort region.

This volume will not only delight the pure naturalist but win the gratitude of every experimentalist and ecologist, for it is evident that many old confusions have been cleared up, the known range of many species extended, more than one taxonomic misalliance corrected, and a clear, comprehensive, and useful picture of the group presented. Much remains to be done in this and other groups and it is greatly to be hoped that the Duke University Marine Station will issue subsequent volumes of a similar nature.

GAIRDNER MOMENT

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BIBLIOGRAPHY OF BIOGRAPHIES OF ENTOMOLOGISTS. *The American Midland Naturalist, Volume 33, Number 1.*

By Mathilde M. Carpenter. The American Midland Naturalist, University of Notre Dame, Notre Dame, Indiana. 75 cents (paper). Pp. 1–116. 1945.

The title of this work clearly indicates its scope and usefulness. The author states in the introduction: "The references include not only obituaries, but birthdays, portraits, anniversaries, biographies and disposition of collections." The labor involved in the preparation of this extensive work must have been great and one wonders if it was worthwhile.

ROBERT MATHESON

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COMMON INSECTS OF HAWAII.

By David T. Fullaway and Noel L. H. Krauss. Tongg Publishing Company, Honolulu, Hawaii. $3.50. 228 pp. 1945.

The title fully indicates the contents. The authors give an approximate census of the known insects of the Hawaiian Islands, indicating the number known to be endemic and those introduced. The first chapter gives a very brief account of insect structure and metamorphosis. The following eight chapters deal with the various orders, the authors selecting certain families and species for discussion. Every species discussed is illustrated on one of the plates. The size of each insect illustrated is shown by a line placed beside the picture, and this is a valuable feature. Unfortunately the colored plates are not all that they should be, but they give a fair representation of the form being discussed. The last chapter discusses the relatives of insects, such as the mites, spiders, scorpions, pillbugs, sowbugs, centipedes, and millipedes. These are illustrated in black and white. The book should prove of value to the people of Hawaii, as most of the insects described and figured are of economic importance.

ROBERT MATHESON

A GUIDE TO THE STUDY OF DRAGONFLIES OF JAMAICA. *Bulletin of the Institute of Jamaica Science Series, Number 3.*

By Francis Cecil Whitehouse. The Institute of Jamaica, Kingston. 1s. 6d. (paper). 69 pp. 1943.

This is a list of dragonflies collected by the author between November 1941 and May 1942. To this list are added all species previously recorded from the island. The author gives notes on habits and habitats of the species collected, with brief characters for field identification and places of collection. The publication provides a brief handbook of the dragonflies of Jamaica.

ROBERT MATHESON

THE MOSQUITOES OF NEW JERSEY AND THEIR CONTROL.

By Thomas J. Headlee. Rutgers University Press, New Brunswick, New Jersey. $4.00. x + 326 pp. 1945.

T. J. Headlee is to be congratulated upon issuing a new and complete report on the mosquitoes of New Jersey, their biologies, habits, and habitats, and up-to-date methods of control devised through long years of experience. The original report by John B. Smith (1904) was a classic on mosquito biology and methods of control. Headlee has brought it down to date.

The opening chapter stresses the value of control, and the last chapter presents in summary form the increased valuation of taxable lands due to mosquito reduction. The other chapters bear the following titles: Structure, Classification and Keys; The New Jersey Mosquito Fauna; Mosquito Biology; Influence of Environment; History of Mosquito Control in New Jersey; Principles and detailed Procedure of Mosquito Control; Larvicides; Mosquito Repellents; Laws relating to Mosquito Control.

The titles clearly indicate the scope of the work. Chapter 3 consists of only a list, presented in tabular form, of the trap collections of female mosquitoes for the ten year period, 1932 to 1941. The chapter on mosquito biology, the longest in the book, is largely taken from the work of John B. Smith. The chapter on the influence of environment is restricted almost entirely to the conditions obtaining in New Jersey, with no mention of the extensive work done in this field by many workers in this and other countries.

In chapters 7 and 8 the reviewer had anticipated a fuller account of the principles of mosquito control, and of larvicides. Both chapters are brief and have but few illustrations of the machines and methods so successfully developed in New Jersey, except in some of the plates which are not referred to in the text. The discussion of the development of new machinery and its usefulness is very brief.

The illustrations, except the sixteen plates, are nearly all from the report of John B. Smith. Unfortunately there is no index, and the bibliography is very brief. The printing is well done, but the paper is not of the quality one could wish for such a work. There are a number of obvious errors, but these do not detract from the usefulness of the work. The volume should prove of great value to all those interested in mosquitoes and their control.

ROBERT MATHESON

STUDIES ON THE ANOPHELINE COMPLEX OF WESTERN AMERICA. *University of California Publications in Entomology, Volume 7, No. 11.*

By Thomas H. G. Aitken. University of California Press, Berkeley and Los Angeles. $1.25 (paper). Pp. 273–364. 1945.

This is an elaborate and detailed study of the anopheline complex of western America. No adequate summary can present these painstaking, detailed studies on the morphology and biology of the adults, larvae, and pupae of the species and varieties discussed. Each species is dealt with in great detail. The author concludes from his studies that the following may be considered to constitute the complex: ***Anopheles maculipennis occidentalis*, *A. maculipennis freeborni*, *A. pseudopunctipennis franciscanus*, *A. pseudopunctipennis franciscanus*** var. ***boydi***, and ***A. punctipennis***. Keys are given to the females, males, larvae, pupae, and eggs of the forms indicated above. There is an excellent discussion of the distribution of these anophelines, and there are many illustrations supporting the views held by the author as to the relationship of these forms. An excellent bibliography completes the paper.

Robert Matheson

A Systematic Study of the Pacific Tunas. *Fish Bulletin No. 60.*

By H. C. Godsil and Robert D. Byers. State of California Department of Natural Resources, Division of Fish and Game, Sacramento. Free upon request (paper). 131 pp.; 2 plates. 1944.

In order to clarify the differences among the tunas of the Eastern Pacific specimens were dissected and their morphology compared. Whenever possible, representatives from the Western and Mid-Pacific areas were similarly studied. It is concluded that the skipjack, the yellowfin, and the albacore of the Eastern Pacific are similar to those of Japan and the Hawaiian Islands. The bluefin tuna of Southern and Lower California are the same and are temporarily assigned to the same species as *Thunnus thynnus* of the Atlantic. Lacking Japanese material for direct comparison, the bluefin of Japan has been considered separable. The existence of a fifth species, here called the big-eyed tuna, is confirmed.

For each of the five forms, measurements are given in tabular form, with descriptions of the external appearance, the teeth, tongue, branchial assembly, viscera, skeleton, and excretory and circulatory systems. The appearance of the viscera *in situ* was found to be the most valuable and infallible character for identification; specific differences were also found in parts of the circulatory and excretory systems. Without further material, no nomenclatural revision was considered advisable; and in this respect, the work of Kishinouye has been followed.

Henri C. Seibert

Modern Bird Study.

By Ludlow Griscom. Harvard University Press, Cambridge, Massachusetts. $2.50. x + 190 pp. 1945.

A lot of interesting and useful information gathered from the field of modern ornithology is presented here by the well known American ornithologist, Griscom. The first chapter traces the change of ornithological study from the days of collecting and classification to modern field investigations emphasizing the living rather than the dead specimen. The next chapter, on capacity and intelligence in birds, includes many examples of bird behavior that tend to prove a limited intelligence. Beyond this point, no other interpretations on the observations are submitted. Chapter III, on the adaptability of birds, provides examples to show that "birds run the entire gamut between extreme specialization and great adaptability." In the former category are birds that are being, or have been, extirpated through the agencies of man, with others that are suffering from competition by introduced species. To the second group belong those birds, such as the barn swallow and robin, that have become more or less domesticated. The interesting observation is made that in new and quickly exploited countries, like North America and Australia, several kinds of birds are approaching extermination, while in older countries, like Britain, practically all species continue to exist, though some may have been greatly reduced in numbers over a long period of time. The causes and routes of migration are discussed in two chapters, followed by four chapters on distributional problems in South, Central, and North America, areas with which the author has had the greatest experience. The final chapter is concerned with classification and speciation.

The book is an outgrowth of a series of lectures, with the subject matter somewhat revised and expanded. The presentation is informal and affords extremely pleasant reading. The limitation of subject matter is certainly the author's choice, but the reader should not be misled by the title into thinking that all or even a large part of modern bird study has been considered. In the discussion of subspecies, the statement that "in all scientific works and articles the correct subspecies name must be given" is certainly open to question, depending on the type of work presented. In describing the eastern and western flickers,—"one has yellow wing linings and tail feathers and red moustache stripes; the other has red linings and tail feathers and black moustache stripes"—the author has apparently made a slip, although one is led to believe that this error is duplicated previously where a red facial stripe is mentioned in connection with sex recognition. If reference is made to Noble's experiment (as indicated in the bibliography), the eastern species with black moustache is meant. The chapter on capacity and intelligence leaves the reader uninformed as to why birds act as they do, no mention being made of modern concepts of bird behavior. The reader, however, should not be deterred by these minor faults and personal criticisms, for this little volume is to be heartily recommended as worth-while reading for all students of birds.

Henri C. Seibert

The Distribution of the Birds of California. *Cooper Ornithological Club, Pacific Coast Avifauna, Number 27.*

By Joseph Grinnell and Alden H. Miller. Cooper Ornithological Club, Berkeley. $7.00 (cloth); $6.00 (paper). 608 pp.; 1 plate. 1944.

This handsome and excellently printed volume was begun and half-way completed by the late senior author, while Miller has finished the task and revised the entire manuscript. It is an outgrowth of Grinnell's *Distributional List of the Birds of California* published in 1915. All species and subspecies "that are proved to have occurred naturally in the wild and within historic times in the State and of which at least one specimen has been preserved or verified as to identity by some ornithologist" are first listed systematically. This list, following the above criteria for inclusion, consists of 644 species and subspecies (427 species). An attempt has been made to standardize vernacular names by giving one name for the species as a whole and by adding a further descriptive name for the subspecies.

The main part of the volume gives, for each bird, its synonyms, status, geographic range, habitat, along with editorial notes. The synonyms apply only to names used with reference to California, listed chronologically, but with no citations. Under "status" are comments on seasonal occurrence, migration, relative numbers, and any definite changes in numbers and range recorded in historic times. The paragraph on range includes a complete and detailed listing, with references, of locality records, a certain amount of selection having been made in these records to avoid duplication. The notes refer mostly to nomenclatural departures from the A. O. U. check-list and to other taxonomic data.

Whenever more than one subspecies of the same species occurs within the boundaries of the State, a distributional map is provided showing the spots where breeding or resident specimens were collected. Because of the topographic variability of California, its proportion of geographic races is very high (fourteen subspecies of the song sparrow alone), and consequently the number of these useful maps is considerable. The supplementary list includes all those species that have been reported from California, whether correctly or incorrectly, but which do not pass the test as previously quoted. This list therefore includes sight records, introduced species, and those of doubtful occurrence. There is a complete index to bird names. This volume is indeed a fine piece of workmanship, showing the results of years of faithful amd careful compilation of records, and it will remain a standard reference for California ornithologists for many years to come.

Henri C. Seibert

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Birds of Georgia. *A Preliminary Check-List and Bibliography of Georgia Ornithology. Sponsored by the Georgia Ornithological Society as Occasional Publication No. 2.*

Compiled by Earle R. Greene, William W. Griffin, Eugene P. Odum, Herbert L. Stoddard, and Ivan R. Tomkins, with a historical narrative by Eugene E. Murphey. University of Georgia Press, Athens. $2.00. 111 pp.; 1 plate. 1945.

This publication is intended to serve as a preliminary check-list and bibliography of the birds of Georgia. To this end the five compilers have made an excellent contribution. Eugene E. Murphey has contributed a review of the history of Georgia ornithology. The bibliography is extensive and includes all articles dealing with or mentioning in part, birds studied or collected within the State. The birds are listed systematically, together with a brief statement on their abundance and distribution. The hypothetical list includes hybrids and forms of doubtful status. There is an appendix of Georgia bird clubs, a bibliography of local lists, and a map of the State with brief comments on its physiographic regions.

Henri C. Seibert

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Bird Portraiture. *"How to Do It" Series Number 35.*

By C. F. Tunnicliffe. The Studio, London and New York. $3.50. 96 pp. 1945.

This is by far the most inspiring book on wildlife drawing that the reviewer has seen. Although designed for the beginner, an undeniably greater service has been rendered the experienced bird artist who needs exciting fare to incite him to try new ways of doing things. I, for one, expect that my own drawings will reflect some of the things Tunnicliffe has suggested. I showed the book to Major George M. Sutton, one of our "modern Audubons," and he was as enthusiastic as I. He said that although he had not thought of Tunnicliffe as one of Britain's best bird painters, he would unqualifiedly rate him so after glancing at this book.

Tunnicliffe advises the beginner to draw constantly from life, starting with domestic fowl, then working at the zoo. Some knowledge of a bird's skeleton and main feather groupings should be learned at this point. It is here that Tunnicliffe could have given the beginner more help by indicating in his sketches and diagrams some of the simple mechanical rules of bird feather arrangement that are so valuable to know—that most birds have twelve tail feathers, in two groups of six; that the central two feathers are on top and the overlapping is from the center outward. Also that on the upper surface of a bird's wing the primary feathers overlap on the front edges, while on the under-side of the wing they overlap on the rear edges. I had been drawing birds for several years before I learned that the median coverts overlap in the opposite direction to the secondary coverts.

Knowing these rules of thumb makes bird drawing much simpler.

Graduating from the barnyard and the zoo to quick-moving birds in the field is the next step. The author instructs the learner to "watch and watch and watch again. Do not draw while the bird is in view but try to get accurate impressions photographed on your mind, then sketch." He advises the careful study of birds found injured or dead, making measured drawings of upper and under tail surfaces, top and side views of beak, wing open, under surface of wing, etc. He suggests the careful study of some of the best bird artists, particularly the Chinese and Japanese masters, Audubon, and Liljifors the Scandinavian.

The book is lavishly decorated with fifty illustrations, many of them in black and white, some in color. These range from decorative spots to compositions where realism is the keynote. Several designs have an unmistakably Oriental flavor. I wish Tunnicliffe had told us precisely what medium was used in the various drawings and also something about the reproduction. He is obviously a master of wood-engraving, but one cannot tell whether some of the black and whites were done in this difficult medium or on scratchboard.

Bird Portraiture is a delightful book to own, to handle, and to read, not only for the artist and the student of birds but for anyone with curiosity and an eye for beauty.

ROGER TORY PETERSON

* * *

MAMMALS OF THE PACIFIC WORLD.
By T. D. Carter, J. E. Hill and G. H. H. Tate. The Macmillan Company, New York. $3.00. xvi + 227 pp. 1945.

This semi-popular small hand-book is issued under the auspices of the American Committee for International Wild Life Protection as one volume of a planned "Pacific World Series." Even though most our armed forces will soon return from the vast Pacific regions and thus lose interest in the details of nature peculiar to the Pacific World, this book will retain its value for many scientists as a convenient and authoritative compilation and condensation of the widely scattered literature on the mammals that live on the innumerable islands of the world's largest ocean.

After a brief introduction, dealing with the distinctive characters and the classification of mammals, the great numbers of mammalian species of the Pacific area are concisely described in taxonomic order and with the avoidance of technical terms and details as far as possible (generic names are given in parentheses, and family- and order-names are mentioned in sub-titles). A third, short section of the book is devoted to the distribution of mammals in the Pacific regions, with a brief discussion of the origin, evolution, dispersal, etc., of these animals. Four pages deal with the preservation, collection, and study of mammals. There follows a brief glossary of unavoidable technical terms and, finally, an alphabetical Index-Checklist of the mammals inhabiting each island or island group. This last part, comprising 38 pages, is particularly welcome for convenient reference. The authors mention, however, that this list may still be incomplete, "due to our lack of knowledge or collecting," and appeal to the reader to report any mammal encountered on a particular island that is not contained in this list under the name of the island. The 69 illustrations are adequate, but might have been more clearly reproduced.

A. H. SCHULTZ

* * *

THE SQUIRREL BOOK.
By Phyllis Kelway. Wm. Collins Sons and Co., London and Glasgow. 4s. 78 pp. 1944.

This is a delightful story of two wild squirrels, Yump and Nuffles, found when babies and raised to adulthood by the author. Her keen observations, her patience, sympathy, and real understanding in dealing with animals are reflected not only in the narrative itself but also in the unusually attractive photographic illustrations accompanying the text. The book is quite superior to the general run of animal stories.

* * *

THE OTTER BOOK.
By Phyllis Kelway. Wm. Collins Sons and Co., London and Glasgow. 4s. 144 pp. 1944.

Phyllis Kelway writes truly delightful descriptions of nature and vivid, lively accounts of animal ways. This story of the tame otter and its simple yet exciting adventures will be sure to keep its readers engrossed. The narrative device of allowing the otter to talk is a dangerous one, but the author has kept skilfully within bounds. The otter remains an otter, a mammal of distinct intelligence comparable to that of a dog, if of its own peculiar turn. The book is beautifully illustrated with pen and ink drawings and with eighteen photographs that must be ranked among the finest animal pictures ever taken.

ANIMAL EMBRYOLOGY

THE INDIVIDUAL IN SIMPLER FORMS. *University of Oregon Monographs, Studies in Psychology Number 2. By Arthur Russell Moore. University of Oregon Press, Eugene.* $1.25 (paper). x + 143 pp.; 13 plates. 1945.

In considering the nature of individuality in embryogenesis and in animal behavior, the problem of the relation of the parts to the whole is ever present. According to the author, certain misconceptions of the nature of the problem have developed because of the emphasis ordinarily put upon the materiality of the parts. For instance, he thinks that the application of analytical methods in physiology and in biochemistry does not, in a comprehensive way, lead to an understanding of some of the most characteristic manifestations of individuality. It is true that in the field of animal behavior one meets types of conduct which could not have been predicted from the knowledge of the physical and chemical nature of the constituent elements of the organism. The cells which make up the body of a worm are not greatly different from those of the warm-blooded animal; yet there is a wide difference in the degree of complexity of conduct in the two forms. Something more, the author feels, is required to differentiate one organism from another.

This monograph, therefore, is an attempt to show, by illustrative examples, that the emergence of new patterns of form and of behavior is made possible by a third factor, the spatial arrangement of the morphological elements. In other words, one must consider not only the physics and chemistry of the organism, but the geometry as well. "This quality of the ordered arrangement of parts makes possible the development of organs, the specialization of function in differentiated tissues, head-tail polarity, and head dominance. The parts being given, the geometrical ordering of them gives coherence and character (that is to say, integration) to the embryonic development and to the reactions of the organism."

The problem of the meaning of ordered arrangement in giving coherence to the individual is dealt with, in terms of increasing complexity, in Chapters I to VI. After a consideration of the evanescent structure of the naked protoplast, there follows an analysis of the development of the free-swimming embryo in terms of structure and positional ordering of cells. The next step in progression deals with the spatial relations of the central nervous system as necessary factors in integration. Chapter VII is given to a consideration of modifiability of function by various chemical substances having particular qualities, with especial attention to the action of those which are the product of the animal's own metabolism. The final chapter deals with memory as a physiological concept.

The illustrative material is for the most part taken from work done in the author's laboratory (much of the experimental work having been carried out at the Hopkins Marine Station, Pacific Grove). As a whole the material is rather clearly and interestingly presented. While many of the issues are controversial, the viewpoint as set forth by the author is an interesting approach (not altogether new) to the larger, and certainly important problem of organization in form and movement.

MARY E. RAWLES

ANIMAL MORPHOLOGY

A HISTORY OF COMPARATIVE ANATOMY *From Aristotle to the Eighteenth Century.*

By F. J. Cole. Macmillan and Company, London. $7.00. viii + 524 pp. 1944.

Everyone concerned with the structure of animals vertebrate or invertebrate, or with the processes by which science advances will be grateful to the author of this handy volume. It is well to remember at the outset that the period covered by the book ends before the rise of comparative anatomy in the modern sense. Within this limitation Cole has presented a storehouse of information based on a first-hand study of the old masters of anatomy. Included are some 200 figures, many of them full page plates, reproduced from both major and minor anatomical classics. Many of them are inaccessible outside the vaults of a few large libraries, so that it seems a pity that they were printed on such abominable paper.

The general plan of the book centers around the work of twenty-three anatomists arranged in chronological order, although there are final chapters on academies and museums and a brief conclusion. Greek anatomy is represented by Aristotle and Galen. Cole's treatment of Aristotle—presenting selections rather than a a survey of his work—employs the admirable method of following certain problems formulated by the great Stagirite, through many vicissitudes down into comparatively modern times. His treatment of Galen differs from that of some historians who appear afraid lest Galen corrupt their readers. Along with Galen's errors, Cole boldly depicts his many penetrating and accurate discoveries and points out that his work on the nervous system was not superseded until the time of Bell and Magendie.

The anatomists of the early sixteenth century are treated rather briefly, possibly because numerous books and figures are already available for da Vinci, Vesalius, and to a certain extent even for Belon. The main portion of the book deals with the work of investigators of the latter part of the sixteenth century beginning with Coiter, Ruini, Fabricius, and Casserius, and continues down to the end of the seventeenth century. Here the text is ample and the figures are numerous. One cannot help but mention three plates of exceptional beauty from Coiter including his famous figure of the skeleton of the Capuchin monkey, or the all but incredible vascular injections of Ruysch (who even injected the bladders used for sealing museum jars), or Nicholl's figure of the gynandromorph lobster—but of this there would be no end. Those familiar only with

Willis' work on the brain will be surprised by the extent of his anatomical investigations on the oyster, crayfish, and earthworm, then little known "Brutes." Malpighi is extensively though not exclusively represented by his work on the silkworm, which is compared with similar work by Pasteur. The Dutch school of anatomy is covered very fully, especially the work of Swammerdam.

Like many an anatomist, Cole is not averse to a good story, and he proves himself in the great tradition in this respect by leading off with what is perhaps the oldest of such tales—the story about why Democritus, having retreated to the amenities of the local cemetery to pursue his studies in comparative anatomy, was visited by the Father of Medicine. The weakest part of Cole's work undoubtedly lies in his conclusions (fortunately brief), which are set in a hopelessly outmoded late nineteenth century framework. As a whole, the book is a noteworthy addition to the armamentarium of any anatomist who aims to be more than a technician. There is an extensive bibliography of source material.

GAIRDNER MOMENT

ANIMAL PHYSIOLOGY

FRANCOIS MAGENDIE. *Pioneer in Experimental Physiology and Scientific Medicine in XIX Century France.*
By J. M. D. Olmsted. Schuman's, New York. $5.00. xvi + 290 pp. 1945.

In the history of science it is most disadvantageous for a man's reputation either to be the teacher or to be the pupil of a very great man. In such a case all that is remembered of him is in general that he was "the teacher of . . ." or "the pupil of . . ." This effect is very strikingly observed in the reputations of Claude Bernard's teacher, Francois Magendie, and of his pupil, Paul Bert. J. M. D. Olmstedt, professor of physiology at the University of California, to whom we owe already a most excellent biography of Claude Bernard, shows in this new biography that Magendie is very much worth remembering for his own sake. He was actually the initiator of experimental pharmacology and of experimental physiology that led beyond the most brilliant accomplishments of the great contemporary French clinicians. Olmstedt gives us a full view of Magendie's many-sided work and life, of his strange education and character, and he devotes considerable space to the famous Bell-Magendie controversy.

One often feels inclined to complain that the history of science is written to so great an extent in the form of biographies. But if all biographies were to be such as this, there would be no reason to complain. Great readability is obtained, though all cheap effects are avoided. Personal and scientific details, general historical background, and specific medical data are all well balanced in their proportions. It is one of the very few books one enjoys reviewing.

ERWIN H. ACKERKNECHT

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THE HUMAN BODY. *Fourth Edition.*
By Logan Clendening. Alfred A. Knopf, New York. $4.00. xv + 443 pp.; 20 plates. 1945.

It is natural to wish to have a special word of kindness for this final edition of the late Kansas doctor's book on the fundamentals of human anatomy, physiology, and pathology. This is unfortunately hardly possible. Changes from the previous edition have been very minor ones. Most of the old errors remain uncorrected, and they are not few in number. However, *The Human Body* is still one of the outstanding books of its kind, and if the virtues of the final edition are those of its predecessors, they are not slight. Few biological books have been written with more humor or more zest. Few have less of the musty flavor of scholastic learning, or so sharply prick and puncture the foibles and misconceptions of laymen and doctors alike. Few are so likely to encourage in their readers as lasting a taste for knowledge of their physical selves, or as eager a curiosity to pursue further the study of life.

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LECTURES ON THE KIDNEY. *Porter Lectures—Series IX; The William Henry Welch Lectures.*
By Homer W. Smith. University Extension Division, University of Kansas, Lawrence, Kansas. $1.00. 134 pp. 1943.

Three of the lectures which comprise this book were delivered at the University of Kansas School of Medicine in 1939 as the Porter Lectures. The content of these lectures is indicated by their titles: The Evolution of the Kidney; Newer Methods of Study of Renal Function in Man; and The Renal Blood Flow in Normal Subjects. The remaining two chapters of the book are entitled: Renal Physiology Between Two Wars; and The Application of Saturation Methods to the Study of Glomerular and Tubular Function in the Human Kidney. These two lectures, the William Henry Welch Lectures, were delivered at the Mount Sinai Hospital, New York City, in 1943. The summary of the probable course of development of the kidney elements as found in mammals, reptiles, teleost, and elasmobranch fishes is very interesting and convincing. In section four the author relates how the peculiarities of kidney structure and function in various species have been used to clarify the mechanism of function of the mammalian kidney. This account of the progress made since 1917 is very interesting and instructive. The subject matter of sections two, three, and five has become well known to physiologists, and much of the material has been incorporated in recently revised textbooks. These three lectures, however, present the information obtained in recent studies of the kidney much more clearly and fully than do textbooks and numerous recent reviews. The last of the sections deals principally with the problems presented by possible intermittency of glomerular activity and tubular perfusion, which may occur in the human kidney. It is a detailed account of modern methods of studying human kidney function and the information that has been obtained by means of these techniques. This small volume of lectures is recommended to those interested in the physiology of the kidney and the cardiovascular system.

CHANDLER McC. BROOKS

RECENT ADVANCES IN ENDOCRINOLOGY.

By A. T. Cameron. The Blakiston Company, Philadelphia. $5.00. vii + 415 pp. 1945.

The preface of the first (1933) edition of Cameron's *Recent Advances* presents endocrinology as a biochemical subject to the degree that "the precise truth of its teachings depends ultimately upon the isolation of the different endocrine principles in pure crystalline form, so that their physiological and pharmacological properties may be ascertained accurately . . . the final problem, the elucidation of the precise mechanism of the actions of these principles will require profound and prolonged biochemical and physiological study." It is further stated that clinical medicine shares with physiology, biology, anatomy, and pathology the task of indicating methods of test whereby these ends may be achieved. In the present edition, it is stated that "at the suggestion of the publishers, the clinical aspects of endocrinology have received more attention . . . and the volume has had to be almost completely rewritten." The result is a volume that diverges considerably from its title, and also from the council of perfection originally set for it; it is, and can be recommended as, a textbook of clinical endocrinology.

A real attempt appears to have been made to digest the recent literature, as for example, in the sections on hyperthyroidism, cardiotoxic goiter, panhypopituitarism, and adrenocortical syndromes. The section on chemical transmission of nerve impulses, however, has been carried over from a previous volume and ignores recent and exciting developments in this subject. Alloxan diabetes managed to squeeze into this volume, but much work evidently arrived too late for inclusion.

The custom of treating the endocrine system by "glands" dies hard; the author's present section on "Integration of the action of hormones associated with reproduction" and the chapter on "Cushing's Disease and the Adrenocortical Syndromes" represent successful attempts to escape the glandular incubus.

The second "fundamental concept" of the author, that a gland may produce too much or too little of a specific compound, but that it does not produce abnormal compounds, has served a useful turn, especially in reference to abnormal thyroid states; but in view of the work of Rhoades et al. some modification of this dictum may be necessary. Steroid compounds (hormones?) arise in adrenal dyscrasias and in cancer which are apparently absent in normal individuals.

H. R. CATCHPOLE

ANIMAL NUTRITION

NUTRITION WITH SENSE.

By Eleanora Sense. M. Barrows and Company, New York. $2.00. 222 pp. 1944.

A complete knowledge of nutrition includes not only an understanding of the daily food requirements for the human body, but also a comprehension of the need for careful selection and preparation of the available foods, as well as their nutritional values, in fulfilling those requirements. The present volume is designed to furnish just such a complete and up-to-date knowledge of nutrition for the average home-maker.

The basic foods (proteins, carbohydrates, fats, vitamins, and minerals) are in turn discussed in the light of body needs, food sources, and a daily nutrition menu pattern. The importance of obtaining sufficient quantities of the various food elements in the proper combinations to maintain vigorous growth in children and general good health in adults is stressed throughout the text. Emphasis is also placed on methods of preparing foods, not only for conserving the vital food values, but also for combining them into attractive and appetizing meals. Excellent chapters are included to cover such pertinent topics as nutrition in relation to soil and methods of agriculture, economical food marketing and buying, as well as rules for cooking. The latter half of the volume is devoted to carefully prepared menus and recipes. A table of food values, a subject index, and an index for menus and recipes are appended.

The work will undoubtedly find popular favor on the high school or college home economics reference shelf, as well as in the home kitchen library.

B. AUBREY SCHNEIDER

CELL PHYSIOLOGY

THE PERMEABILITY OF LIVING CELLS. *Protoplasma-Monographien Volume 19.*

By S. C. Brooks and Matilda Moldenhauer Brooks. (Gebrüder Bornträger, Berlin-Zehlendorf); J. W. Edwards, Ann Arbor, Michigan. $5.00. xviii + 395 + 14 pp. (1941); 1944.

The integrity of its plasma membrane is fundamental, not only to the physiological activity, but to the very existence of the cell, and consequently any experiments or theories that lead to information regarding the intimate nature of this membrane are of great interest to all workers in the biological field. The existence of the membrane is primarily inferred from the differential rates of penetration of substances into the cell, and this characteristic, the permeability of the cell membrane, still remains the most important index to the structure of the plasma membrane, in spite of the contributions of x-ray diffraction, surface tension, electric impedance, and electron microscope studies. The appearance of a new monograph on the permeability of cell membranes by such well known authorities as S. C. Brooks and M. M. Brooks will therefore be viewed as a welcome contribution to this involved subject.

The book was completed in 1939 and unfortunately, as it turned out, was sent to Germany for publication, so that the war effectively prevented its distribution outside Germany. The present edition is an American (J. W. Edwards) lithoprinted reproduction of the German edition and, as such, exhibits numerous technical defects attributable to the difficulties of war-time printing in Germany, e.g., misprints are disturbingly frequent and, every few lines, there is an instance of defective type; on page 31 there is a reference to a non-existent table, and so on. The book thus appears some six years later than the authors intended, and in a cruelly mutilated form.

In the preface, the authors tell us that they had started out ambitiously to cover the whole of the factors involved in the study of permeability, but that only a fraction of what they desired to present had finally come out of their past hopes. They conclude with the statement: "And so we have finally attempted to crystallize into a critique a few of the factors which we have deemed important in connection with the present-time experimental inquiry into Permeability." In reading the monograph, it will be necessary to bear this concluding statement well in mind, for otherwise one may be disappointed, since very many aspects of permeability have either been summarily dealt with or ignored altogether.

The book may be divided into three main parts, consisting of discussions of osmotic phenomena in cells and tissues, of the permeability of cells and tissues to strong electrolytes, and of the permeability to dyestuffs. Chapters on the permeability to non-electrolytes, weak electrolytes, and gases are included in the book, but it is clear from their perfunctory nature that the authors had not their hearts in this part of their enterprise.

To that part of the book dealing with osmotic effects, the reviewer is happy to give warm praise; it is an excellent review of the literature on water exchanges in a wide variety of cells and tissues, viewed both from the (static) equilibrium and the (kinetic) permeability aspects, and the problem of "bound" water is handled with astute critical ability. A minor criticism is that, in dealing with the osmotic "anomalies" of the erythrocyte, the authors, while adducing a lot of material of questionable scientific value, ignore more modern chemical studies bearing on the problem; moreover, their tentative explanation of the anomalies on the basis of electro-osmosis, in consequence of the thermodynamic potential across the membrane, appears to the reviewer very questionable.

The chapter on strong electrolytes is obviously a labor of love; it concerns a branch of the permeability problem with which the authors have been intimately connected for many years and one on which they can speak with authority, yet to the reviewer this chapter is less satisfactory. There are references to the Brooks' theory of accumulation, but this is developed and presented in so obscure a manner that the reader is left with only a vague idea of its essentials and its relation to other theories and the established facts. The permeability of cells to strong electrolytes is very frequently bound up with secretory processes, i.e., the driving force impelling the electrolyte to move is not necessarily the difference in observed activity between cell and surrounding medium. The simplest and most illuminating studies of ionic permeability must therefore be those concerned with ions not greatly, if at all, connected with secretory processes. The erythrocyte probably approaches such a system better than any other cell, but the authors have paid it very scant attention. The result is that ionic permeability, as such, and ionic accumulation are indissolubly mixed in their treatment, and the issue is confusing, especially to the uninitiated reader.

The section dealing with dyes is thorough, and the pages are crowded with references; to those biological workers whose interest in permeability is mainly due to the practical problem of vital staining, it should be invaluable. In the opening paragraph, the authors criticize very forcibly the limitations of dye techniques in permeability studies and seem to be under no illusions as to the illogicality of devoting special chapters to work involving these substances, and it seems unfortunate that they bowed to convention to the extent of devoting some 80 pages to this topic. It is unfortunate because this procedure has led them to discuss the various theories of membrane structure and permeability in an atmosphere tainted by the unreliable nature of much of the experimental work; it would surely have been more satisfactory to have discussed these theories in the light of the more recent quantitative studies on non-electrolytes. As it is, the chapter on non-electrolytes consists of a perfunctory 20 pages and, as if it had not been robbed enough, the important work of Collander and Bärlund on non-electrolytes has been included in the chapter on strong electrolytes.

The book, as a whole, shows unmistakeably that the authors have been at great pains to collect and sift the literature dealing with those aspects of permeability that have interested them most, and they have, moreover, shown no hesitation in frankly and fairly criticizing work which they considered bad. The defects in the book, as the reviewer sees them, lie chiefly in the mode of presentation—the thread of an argument is broken by the indiscriminate lumping in of facts which might have been postponed to a more appropriate place; the important difference between equilibrium conditions and permeability processes, although doubtless clearly appreciated by the authors, are obscured by the failure to discuss these in separate chapters; the problem of secretion should have been kept separate from that of simple permeability; the material dealing with the penetration of non-electrolytes should have been kept separate from that dealing with the effects of non-electrolytes on permeability; and so on. In consequence, the book is of value to the expert interested in one or all of the three aspects of permeability on which the book concentrates. To the teacher of biology or the graduate student, searching for a guide through the complex maze of permeability literature, it offers but meagre aid.

Hugh Davson

BIOCHEMISTRY

The Specificity of Serological Reactions. *Revised Edition.*

By Karl Landsteiner. With a Chapter on Molecular Structure and Intermolecular Forces by Linus Pauling. Harvard University Press, Cambridge, Mass. $5.00. xiv + 310 pp. 1945.

The German and the first English editions of this book received brief mention in these columns, whereas the present edition has been considered by the editors as warranting a more detailed review. This does not reflect any basic changes in the book, which has been considered a classic since its first appearance; rather, it illustrates the enhanced interest in serological phenomena among biologists. Biology is dominated by problems of specificity; the two main approaches now available to interpret specificity on a chemical or physico-chemical basis are those of enzymology and serology. The last fifty years have seen serology grow out of its bacteriological childhood into a full-fledged branch of the biological sciences. The interest of geneticists, in particular, has recently been heightened by the work of Irwin and his group, suggesting a direct relationship between genes and cell antigens. The hypothesis that antigens may represent complete or partial replicas of genes has directed attention to the possibility of modifying the genes by means of antibodies against cell antigens; reported successes along these lines by Guyer and Smith on lens defects in rabbits, and more recently by Emerson on *Neurospora*, await more extensive confirmation.

This second English edition of Landsteiner's book appears after the death of the author, who has more than any other worker been responsible for the development of its subject matter. It is interesting to recall that, while Landsteiner's discovery of the blood groups in 1900 started serology on its way toward wider biological applications, his work on artificially synthesized antigens, begun in 1914, gave it a solid chemical foundation. In the present edition, most chapters are amplified and two new chapters are added *ex-novo*. The result is a most comprehensive discussion of present-day ideas of serological specificity and of their historical development.

The serological specificity depends on and closely reflects the chemical structure of the antigens is now an established fact. Specificity can be traced to certain determinant groups of various degrees of complexity, which the antibody supposedly "fits" as a key fits a lock. All serological reactions are considered as due to specific attraction between antigen and antibody, with the limitation that antibody "specificity" is directed toward the determinant groups rather than toward the antigen as a whole. Cross-reactions may arise either from the sharing of common determinants by two antigens, or by structural similarity of determinants, in which case specificity generally takes the form of stronger affinity of the antibody for the homologous antigen.

The physical basis of this affinity, and its relation to the mode of antibody production, have recently received an appealing interpretation by Pauling. Antibody formation is considered as being due to the folding of the plastic polypeptide chains of the globulin molecule in such a way as to fit the mold provided by the active groups of the antigen surface. The resulting complementariness of surface patterns then permits a relatively large portion of the surface of antigen and antibody to be brought together at very close range. Specific attraction reflects the specificity of the patterns, and results from the summation of numerous aspecific forces between atoms and groups of atoms thus brought into play. Biologists will welcome the inclusion in this edition of a chapter by Linus Pauling, in which he summarizes the nature of intermolecular forces and briefly indicates how they may be supposed to act in antigen-antibody reactions. This summary, very clear and to the point, will help those who do not feel equipped for the study of more complete treatments of this topic.

For the biologist, some of Landsteiner's conclusions regarding natural antigens and species specificity are worth analyzing more closely. In the words of the author, "... there exist two systems of species specificity in the animal kingdom, the specificity of proteins and that of cell haptens. The proteins, it would seem, undergo gradual variation in the course of evolution, while haptens are subject to sudden changes not linked by intermediary stages." Typical of cell haptens are, for example, the blood group substances and in general the red blood cell antigens, and the Forssman antigen. It is to be expected that the relatively small, highly active groups responsible for cell hapten specificity would show serological variation in discrete, well defined steps, since allelic differences in one or sometimes a few genes may deeply affect their relatively simple structure. Cross-reactions between physiologically or systematically unrelated cells are also to be expected, since antibodies against small, very active determinant groups often give marked cross-reactions with chemically related haptens, such as may be present in very different cells.

The supposedly "gradual" systematic variation of proteins might appear more difficult to reconcile with our current ideas of evolution by accumulation of discrete genetic changes. On the one hand, however, the work of Cumley and Irwin on serum proteins in species hybrids of doves seems to indicate that, as in the case of cell antigens, species differences in protein antigens may be reducible to discretely segregating units. On the other hand, protein variation within a species and between species may actually occur discontinuously, by discrete changes, even when serological tests do not indicate it. Serological analysis, though a very refined tool, lays no claim to finality. For proteins, in particular, we generally consider the antigenic determinants as large areas of the molecular surface, whose overall configuration, rather than one or a few strongly active groups, is responsible for serological specificity. Changes in one or two groups may affect only slightly the specific reactivity of the overall pattern, as indicated also by experiments with polypeptides. If we imagine that a large number of genes are involved, through a number of enzyme systems, in protein synthesis, it is not strange that *serologically detectable differences* only appear after a relatively large number of genetic changes have taken place. It should be added that if sudden major changes in protein structure occur, they may have a lower survival value due to the delicate functional test to which most proteins are subject in the organism. This need not be so for some cell haptens, as for instance in the case of the blood group substances, which as yet have not been found to perform any important function.

The serological specificity of physiologically different proteins, like hemoglobin, serum albumin, and keratin, is simpler to interpret, because of known differences in their chemical composition. It is, however, intriguing that detectable antibody formation rarely follows the injection of any protein from the same species or individual. One does not feel entirely satisfied with the explanation, very tentatively mentioned by Landsteiner, that in such cases antibodies are actually formed and rapidly fixed by the proteins of the organism itself. On the other hand, it is difficult to see how the antibody-forming cells could recognize every homologous protein antigen, even though each cell has a complete set of genes similar to those which directed the synthesis of the antigen.

A field which seems to have been the object of surprisingly little investigation is that of developmental serology. It seems to the reviewer that various lines of evidence (recapitulation, transplantation, virus research), alike suggesting the possibility that tissue and protein specificity in embryonal life may be different than in the adult, should encourage more work in this field.

It is characteristic of this book that theoretical questions, such as those we have discussed here, are never dogmatically answered nor receive more emphasis than their experimental basis justifies. Cautious warnings as to contradictory findings and alternative interpretations are rather the rule. The enormous wealth of material often gives the book the apparent character of a bibliographical review, in which, however, every result is evaluated, interpreted, and coordinated in a broader picture. This very wealth of material makes the book difficult reading; observations pertinent to one topic are often scattered in different sections, important generalizations buried in the middle of a paragraph. Nor is the reader helped by the rather peculiar system of bibliographic references, or by the extensive use of chemical terminology with little assistance from structural formulas.

The character of the book seems to reflect the character of Karl Landsteiner's life work, probably more preoccupied with an attack upon basic problems in their fundamental aspects than with the attainment of a final, self-contained picture of this or that special problem. It is significant that throughout both this book and the monumental work of its author one can trace, along with the preoccupation with the chemical basis of serological phenomena, a continuous awareness of their biological implications.

S. E. LURIA

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COLLOID CHEMISTRY *Theoretical and Applied. Volume V. Theory and Methods; Biology and Medicine. By Selected International Contributors, collected and edited by Jerome Alexander. Reinhold Publishing Corporation, New York.* $20.00. vi + 1256 pp. 1944.

This weighty volume contains no less than sixty contributions by outstanding authorities on various subjects closely or distantly related to colloid chemistry. It is a volume that will be of special interest and usefulness to biologists, since, in addition to twenty-five contributions dealing with theory and methods, there are thirty-five directly in the field of biology and medicine. Such a wealth of material forbids even a mention by title of all the individual contributions. A few general comments and an arbitrary selection of a few papers for special mention must suffice.

In general, the contributions are of a type more interesting and more valuable than those, for example, in the *Annual Reviews*. Subjects are discussed critically and in a rounded way, the aim not being to cite all recent papers within a limited field but to treat each subject in such a way that a reader of even limited special background might grasp the discussion. One is consequently amply repaid for the slow going throughout these hundreds of closely printed pages. The presence of numerous diagrams and half-tones is helpful, although many of the half-tones are poorly reproduced. Each article has its separate bibliography, some of them listing 100–250 references. There are general author and subject indexes.

In the first section, that dealing with theory and methods, many of the papers will prove over-technical for most biologists. Electron and x-ray diffraction, molecular films, Liesegang rings, polymerization, the electron microscope, cyclotron, betatron, and high speed centrifugation are only a few of the subjects discussed.

Section II, on Biology and Medicine, starts with a fundamental discussion of protein structure by Astbury. Rothemund's review of photosynthesis is helpful in bringing one up to date. Wanda K. Farr makes an exhaustive review of work on the plant cell wall, but helps to confuse terminology by steadfastly calling it the plant cell membrane. There is a very rewarding discussion of enzymes and vitamin action by Axelrod and Elvehjem. Minerals and vitamins in applied nutrition (Booker) is also a mine of condensed information. The discussion of the mechanism of hormone action attempts to look ahead; Kamm and Kitchen, however, have endeavored to adopt a narrow definition of "hormone" that seems so untenable that they were not even able to maintain it consistently themselves. Wald on visual pigments and Hudson Hoagland on chemical pacemakers are both extremely interesting, the latter work on the identification of enzyme systems that are limiting factors or "bottlenecks" in metabolic processes promising great advances in the future. Lauffer and Stanley have contributed a further review on purified viruses, and Jack Schultz a discussion of the gene as a chemical unit. The latter paper will probably be of chief interest to advanced geneticists. Menkin's work on leukotaxine makes an interesting review. Boyd contributes an excellent review of antigen-antibody reactions. Cannon has made a concise summary of homeostasis, while Leo Loeb's review of the causes and nature of cancer is masterly and deserves much fuller comment than it can receive here. A discussion of gerontology (A. J. Carlson) and two interesting contributions on colloidal relations in neuropsychiatric disorders (Spiegel and Spiegel-Adolf; Ludlum) must also be mentioned.

The final contribution deserves a separate word. It is from the long-silent C. R. Plunkett, and is on "The Primary Physicochemical Basis of Organic Evolution." The wealth of original thought, synthesis of ideas, and fruitful hypothesis here can only be appreciated after careful study. To every student of evolutionary process and gene action it is recommended, in the hope that it will prove to be a mental catalyst of superior activity. For this one contribution alone, to say nothing of the great value of the 59 others, one ought to be willing to meet the rather high cost of the volume.

BENTLEY GLASS

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POLYMER BULLETIN. *Published with the cooperation of the Bureau of High Polymer Research, Polytechnic Institute of Brooklyn, New York—Herman Mark, Director. Bimonthly. Volume I, Number 1, April 1945.*

Editor, Paul M. Doty. Interscience Publishers, New York. $2.40 a year; foreign, including Canada, $2.90 a year.

"To provide a medium for the dissemination of information on trends, developments and research in the rapidly growing field of high polymers" . . . "summarizing the seminars and symposia held at the Institute" . . . "news items in this field" . . . "contributed papers."

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REPORTS OF THE BIOCHEMICAL RESEARCH FOUNDATION OF THE FRANKLIN INSTITUTE, *Volume VII, 1942—1943.*

Collected Papers. Biochemical Research Foundation of the Franklin Institute, Newark, Delaware. $3.50. (1944).

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MICROBIOLOGY

CONFERENCE ON GENE ACTION IN MICROORGANISMS. *Special Number, Annals of the Missouri Botanical Garden, Volume XXXII, Number 2, April, 1945.*

The Missouri Botanical Garden, St. Louis. $5.00 (paper). Pp. 107–263. 1945.

This special number presents the papers and discussion of the Conference on "Gene Action in Micro-organisms" held February 2-3, 1945, in St. Louis. Microbiologists, geneticists, general physiologists, and biochemists will find it exceptionally worth their attention. Papers by Demerec, Hollaender, Gowen, Delbrück, and Luria deal with mutations of penicillium, bacteria, and viruses affecting resistance and virulence. Another group of papers deals with gene action. To this group Lindegren and Spiegelman, Tatum and

Beadle, Sonneborn, Greenstein and Chalkley, and Sterling Emerson have contributed. The study of enzymatic adaptation in yeasts, of biochemical mutations in Neurospora, of the killer gene and kappa interaction in Paramecium, and of the differences in effect of ribose and desoxyribose nucleic acids on rates of methylene blue reduction by aqueous extracts of liver have added much to present knowledge of the mechanism of gene action and have added the plasmagene to the concepts that must definitely be reckoned with. Emerson presents a graphic and intelligible theory of gene-enzyme-substrate specificity as related to gene reproduction. These fertile discussions should lead to much productive research.

* * *

THE BACTERIAL CELL *In Its Relation to Problems of Virulence, Immunity and Chemotherapy. Harvard University Monograph in Medicine and Public Health Number 6.*

By Rene J. Dubos, with an addendum by C. F. Robinow. Harvard University Press, Cambridge, Mass. $5.00. xix + 460 pp. 1945.

No phase of bacteriology is more fundamental, nor has interested more investigators in the field, than the bacterial cell itself. The literature which has accumulated is enormous, but there has been nothing available having either the scope or the excellence of this book. It deals with cellular morphology, physiology, and chemistry, with stability and variation, and with the phenomena of virulence, immunity, and antibacterial action in their relation to the nature and organization of cell components. Particularly emphasized are the properties of specificity and variability of the bacterial cell.

The various subjects are developed with discerning clarity. A tremendous amount of diverse material is integrated simply into a concise, intelligible, and thoroughly readable whole—no mean achievement in view of the elaborate vocabularies of the highly specialized sciences concerned. Apparent inconsistencies and inadequacies of present day knowledge are pointed out, as well as conflicting opinions. Lines of thought for future research are suggested. This outstanding book should be read by every bacteriologist, by those interested in the mechanisms of infection and resistance, and by biochemists.

Following the text is an added paper on nuclear apparatus by C. F. Robinow of the Strangeways Laboratory in England. His findings concerning the bacterial equivalent of chromosomes, the nuclear structure of spores, and cell division in the genus *Bacillus* are summarized. The book is attractively illustrated and well indexed; it has a lengthy bibliography.

HARRIETTE VERA

MICROBIAL ANTAGONISMS AND ANTIBIOTIC SUBSTANCES.

By Selman A. Waksman. The Commonwealth Fund, New York. $3.75. ix + 350 pp. 1945.

The comparatively recent and almost explosive development of the field of knowledge of antibiotic action makes this volume particularly useful as a reference for those who have not been especially involved in the investigations. Written from the point of view of the soil microbiologist, the introductory chapters are devoted to that subject, and emphasis, throughout the book, is directed toward it. The reporting of specific contributions, although the results have frequently been contradictory, is detailed and thorough; the bibliography is extensive. The well-planned material on methods and the frequent tables and charts should be exceedingly useful to teachers and to students interested in antibiotics.

The scope of the book is broad. Chapters on the chemistry of antibiotic substances and the nature of antibiotic action are comprehensive, and the limitations of present day information are indicated. Both plant and animal diseases are considered, and the interrelationships of organisms in their habitats are discussed. Considerable material is presented about penicillin and other substances which have been used clinically, but, on the whole, public health aspects are not emphasized. In the concluding chapter problems in need of clarification are brought out, and possibilities for future research are suggested.

A number of photographs are included, and there is an index of microorganisms as well as a more general subject index.

HARRIETTE VERA

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BACTERIOLOGY AND ALLIED SUBJECTS.

By Louis Gershenfeld. Mack Publishing Company, Easton, Pennsylvania. $6.00. xxiii + 561 pp. 1945.

This volume, which is an outgrowth of the author's earlier *Bacteriology and Sanitary Science*, is written primarily for pharmacy students and should serve that purpose adequately. Moreover, it ought to be useful as a text or as a reference for students in other fields related to bacteriology.

A large amount of practical information is included between the covers of this text, and the material selected differs somewhat from that of other similar works. For students expecting to specialize in bacteriology, the treatment of bacterial physiology seems to be rather limited. Such "allied subjects" as insect control, insecticides, fumigation, and biological products, which are often missing or sketchily discussed in most texts, are treated in some detail. Appropriately enough, the section on disinfection is extensive. There is comparatively little of the public health aspect of bacteriology. Illustrations are few and uninteresting. The index is satisfactory.

HARRIETTE VERA

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HEALTH AND DISEASE

SAFE AND HEALTHY LIVING. *I. Spick and Span. II. The Health Parade. III. Growing Big and Strong. IV. Safety Every Day. V. Doing Your Best for Health. VI. Building Good Health. VII. Helping the Body in Its Work. VIII. The Healthy Home and Community. New Edition.*

By J. Mace Andress, I. H. Goldberger, Marguerite P. Dolch, and Grace T. Hallock. Ginn and Company, Boston. I, 84 cents; II, 88 cents; III, 92 cents; IV, 92 cents; V, 96 cents; VI, $1.00; VII, $1.04; VIII, $1.08. I, viii + 152 pp.; II, viii + 184 pp.; III, xii + 252 pp.; IV, x + 258 pp.; V, viii + 298 pp.; VI, viii + 298 pp.; VII, viii + 314 pp.; VIII, viii + 339 pp. 1945.

Attractive, well illustrated, carefully graded books like these should prove to be well liked. To an adult biologist looking back, there may seem to be an undue amount of repetition of subject matter year by year. To the average child this is probably not unduly noticeable, and, of course, a certain amount of review is required for retention. At any rate, my own children like them a great deal.

The books include units dealing in the early grades chiefly with good health habits, and introduce more and more human anatomy and physiology, bacteriology and sanitation as the child's education advances. In Book VIII, for example, there are 12 units, dealing successively with: your health; warmth, light, and air at home; community health; safe water and milk; the safeguarding and preparation of food; community and home cleanliness; buying food and planning and serving meals; communicable disease; insects that transmit disease; taking care of the sick and injured; home safety and first aid; the health of the mind. The treatment of alcohol and tobacco is sane and scientifically sound, avoiding on the one hand the missionary fervor of the prohibitionist and on the other the blindness of those who deny that these drugs create any problem whatever. Books IV–VIII contain lists of suggested books to read, all books have vocabulary sections, and all but I and II have indexes. Tests, exercises, and suggested activities are included; but there is little use of experiment or demonstration, even in the course for the eighth grade. A good teacher, of course, will be able to supply these; but it is disappointing not to find them here, along with so much else that is excellent and thoughtfully planned.

Beginning with Book V, the history of science and medicine as well as that of pertinent social change is successfully interwoven with the discussions of health subjects. Of all the many modern and valuable features of these texts, perhaps this one is most laudable. There is a distinct break with the hard and bitter recollections of the "hygiene" of our own youth as a set of tedious rules.

BENTLEY GLASS

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THE MARCH OF MEDICINE. *Number IX of The New York Academy of Medicine Lectures to the Laity, 1944.*

By Edward A. Strecker, Charles Glen King, Colin M. MacLeod, Reginald Fitz, Sir Gerald Campbell, and Lt. Col. Thomas T. Mackie. Columbia University Press, New York. $1.75. xiv + 121 pp. 1945.

It may be unfair to compare this series of lectures to laymen, given under the auspices of the New York Academy of Medicine in 1944, with the writing on medical topics for the laymen to be found in popular magazines and journals during the same year, as collected, for example, in the *Science Yearbook of 1945*, reviewed elsewhere in this issue. Yet it is obvious that the eminent lectures of this series seem to have had less to say, and have said it more pontifically, than those who undertook to write in simple narrative style for the readers of "Time" or "Collier's." Is it perhaps no more than the effect of a stiff shirt front and a wing collar confronted by orderly rows of faces in a select audience? At all events, once more it has been demonstrated that most lectures make mediocre reading. Not to be hypercritical, however, there is a good deal in these few pages that was worth saying and was indeed well said. For example, to quote E. A. Strecker on the theme of morale and propaganda:

> "It must not be inferred that, in order to be honest, propaganda must confine itself to categorical statements of facts, coldly stated. The natural forte and appeal of propaganda is emotional. However, the emotions are not allergic to the truth, nor do they have an affinity for lies. If anything, they are more deeply moved by the truth. But even the truth must be emphatically, warmly, and stirringly stated."

Other lectures dealt with nutrition (King), chemotherapy (MacLeod), medicine in society (Fitz), the effects of science upon man (Campbell), and war and epidemics (Mackie). The historical account of chemotherapy is especially good.

BENTLEY GLASS

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YOUNG MINDS WITH OLD BODIES.

By Melvin E. Page. Bruce Humphries, Boston; The Ryerson Press, Toronto. $2.50. 184 pp. 1944.

The author of this book claims to have discovered, as a result of a study of dental decay, the basic cause of all diseases. He has also found the method of remedying these basic defects and has published this book solely for the purpose of aiding those who may wish to be aided, and in order that what he has discovered may not be lost.

The first sentence of chapter one is: "Why is it that modern man has a much shorter life span than any other animal?" This, of course, is not correct but it tells one all he needs to know about the book. A good example of the author's method of thinking and his scientific procedures is to be found on pages 26 and 27, where he gives a brief description of his technique of determining endocrine dysfunctions, sympathetic-parasympathetic imbalance, and general metabolism by comparing measurements of the circumferences of various portions of the arm and leg. The book does contain a few well-known truths and some correct statements of fact, but for the most part it is a dismal, uninteresting collection of misconceptions and absurdities. The reviewer does not wish to question the author's right to write a book nor does he wish to criticize the author's desire to aid his fellow men by attempting to cure disease, but such a book as this can be of no value to anyone. Any biologist who reads it will merely acquire a feeling of apprehension for those who need medical aid but who may receive treatment from the hands of unintelligent, uninformed practitioners.

CHANDLER McC. BROOKS

⁂

YOUR HAIR AND ITS CARE.

By Oscar L. Levin and Howard T. Behrman. Emerson Books, New York. $2.00. 184 pp. 1945.

Although it is something of a shock to learn that the scalp and hair are considered as probably the dirtiest and most diseased portions of the human body, it is equally gratifying to learn that they are now receiving some of the personal and professional attention they deserve. In the present volume, two eminent dermatologists have presented, in clear, non-technical language, the latest pertinent information on the physiology, pathology, and care of the scalp and hair.

The point of emphasis running through the entire discourse is that if the scalp is kept clean, and if the general body health and constitution are kept at high levels of tone and function, there is no need to worry about premature baldness or gray hair, unless, of course, there is a hereditary tendency toward such characteristics. Much space is devoted to pointing out the dangers inherent in the misguided use of many of the highly advertised soaps, creams, oils, dyes, endocrine substances, and mechanical devices in attempting to beautify the hair. The beneficial effects of sunlight, x-rays, ultra-violet rays, and vitamins in preserving the hair and in maintaining general good health are emphasized. The latest methods in the treatment of a number of infectious scalp diseases are carefully outlined. A concluding chapter giving questions and answers relating to the care of the scalp and hair and the treatment of numerous scalp disorders encountered in everyday living summarizes the important points brought out in the text.

The work will be read and appreciated, not only by physicians, beauticians, and barbers, but by the general public as well. There is no index.

B. AUBREY SCHNEIDER

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PROFITABLE AND NECESSARIE BOOKE OF OBSERVATIONS.

By William Clowes. Introductions by De Witt T. Starnes and Chauncey D. Leake. Scholars' Facsimiles and Reprints, New York. $6.00. xxviii + 232 pp. 1945.

This facsimile reprint of a book of 1596 deals mainly with two problems still of central importance in war medicine: the treatment of gun-shot wounds and of venereal diseases. Having served with the British army and navy, Clowes had considerable experience in the matter. Though Clowes was no great inventor in the field of surgery, like Paré or Brunschwig, he was an honest craftsman and a good teacher. His numerous case histories, presented in a lusty Elizabethan English, make his book a valuable historical document beyond the narrower field of medical history. The reprint is accompanied by two excellent introductions by De Witt T. Starnes and Chauncey D. Leake. Attention should be drawn to Clowes' treatment of scurvy (p. 40 ff.), one of the earliest "vitamin" treatments on record.

ERWIN H. ACKERKNECHT

⁂

THE ETIOLOGY, DIAGNOSIS, AND TREATMENT OF AMEBIASIS.

By Charles Franklin Craig. The Williams & Wilkins Company, Baltimore. $4.50. viii + 332 pp. 1944.

In 1934 Colonel Craig published a monograph entitled *Amebiasis and Amebic Dysentery*. The present book is essentially a revision of that excellent publication. At the time of the first writing, there was considerable misunderstanding with regard to the symptoms produced by infection with *Endamoeba histolytica*. Although the term *amebiasis* includes amebic dysentery, as only a single manifestation of the disease, the medical profession was more familiar with the latter term. This being the case, Craig at that time included both of them in the title, in order to emphasize the close relationship between the two. It is interesting to note that now only the all-inclusive term, *amebiasis*, appears in the title. This may indicate that the author feels that the lesson taught by the original title has now been amply learned. If this is true, his excellent monograph is largely responsible for this progress.

Shortly before the appearance of the original monograph, the medical profession in this country had been shocked into the realization that not only does amebiasis exist in the United States, but that severe epidemics of the disease can occur in as northern and modern a city as Chicago. With this sobering realization in mind, considerable attention is now being paid to the acquisition of this protozoan infection by service men stationed in tropical countries, and to the possibility of their intensifying this public health problem when they return to this country as carriers of the disease. It is therefore particularly important and timely that Colonel Craig should bring us up-to-date with the facts on amebiasis.

Much information has accumulated during the past ten years that has helped to clarify as well as confuse our understanding of the disease. We are therefore fortunate in having a noted American scientist, with over forty years of experience in the subject, to criticize and evaluate the existing information. The author does not maintain that his book is a comprehensive survey of all the available literature on the subject; however, it is an excellent compilation of original observations and the more significant investigations of other authorities. In some instances, the author tends to present the literature that substantially gives his own opinions, while excluding contradictory evidence. For instance, he makes the statement that infected food handlers are "undoubtedly the most common and most important method of transmission in many localities." In support of this statement, he cites among others the recent observations of Schoenleber (1940). Although this may well be the case, he has failed to mention the careful study of Sapero and Johnson (1939) that minimized the importance of food handlers as transmitters.

The book is written in the same pleasing style and has the same excellent organization that characterized the earlier monograph. The new publication has also approximately the same illustrations as those in the first, but they are not reproduced quite as well. All of the references are placed at the end of the book, preceding the author and subject indices.

M. M. Brooke

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Stitt's Diagnosis, Prevention and Treatment of Tropical Diseases. *Seventh Edition, in Two Volumes. By Richard P. Strong. The Blakiston Company, Philadelphia.* $21.00. xvii + 871 + xl pp.; vii + 872–1747 + xl pp.; 2 plates. 1944.

Since Strong first revised E. R. Stitt's book in 1942, there have been four reprintings and one new edition. This great demand for the book testifies to the excellence of the presentation and the increasing importance of the subject. In this regard, it is well to note the author's statement in the preface to the 7th edition: "The necessity for a new edition emphasizes anew that under the greatly changed conditions of this world and the increased opportunities for the aerial transportation of disease, the medical profession has come to recognize the growing importance of tropical medicine and its world-wide significance and feels that further knowledge and especially the dissemination of new information regarding it is desirable."

There are many small handbooks of tropical medicine but few publications that thoroughly discuss the various aspects of this broad subject. In addition to the essential facts, a great deal of the original literature is here reviewed, enabling the reader to acquire a much deeper insight into the present status of our knowledge and to become aware of the existing problems that are yet to be solved. The thorough presentation of the subject and the dependability of the information has made it the one publication most frequently recommended to the serious student. The tremendous amount of fascinating data that it records makes it a valuable possession of even the specialist in the various fields it covers.

When one considers the caliber of the men responsible for the existence of this book, there is little wonder why it is generally considered to be the finest American publication on the subject. Its basic organization and subject matter were derived from the original work by Stitt that underwent five careful revisions. When Strong rewrote and enlarged Stitt's book for the sixth and seventh editions, he not only added materially from his own wealth of knowledge, but he also obtained assistance and contributions from such outstanding scientists as Bayne-Jones, Meleney, Sawyer, Komp, Russell, Hakansson, Sellards, Simmons, Callender, Shattuck, Sapero, Sandround, Mackie, and Barbour. In addition to this assistance, Strong gives recognition to the fact that he obtained aid from the authoritative works of Craig and Faust, Chandler, Manson-Bahr, and Stitt, Clough and Clough.

The diseases presented in this two-volume publication are those that "occur commonly or most frequently in tropical countries." This does not mean, however, that these diseases occur only in the tropics, for "many of them are encountered from time to time and some are even endemic in countries with temperate climates." For this reason, the whole gamut of etiological agents is considered—protozoa, bacteria, viruses, rickettsiae, fungi, and helminthes. In addition, considerable attention is given to the poisonous plants, fish, snakes, and coelenterates, and to injurious arthropods. Toward the end of the book the author has presented helpful discussions on problems of personal hygiene and medical practice in the tropics.

The appendix includes information on disinfectants and disinfestants, and alphabetically arranged notes on clinical diagnosis and laboratory procedures. Rather extensive lists of references are to be found at the end of each chapter. Unlike some of the other publications that consist of two volumes, the complete table of contents and index are repeated in each volume for the convenience of the reader.

M. M. BROOKE

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ON MODERN SYPHILOTHERAPY *With Particular Reference to Salvarsan.*

By Albert Neisser; translated by Isabelle von Sazenhofen Wartenberg. The Johns Hopkins Press, Baltimore. $1.00. 42 pp.; 1 plate. 1945.

This reprinted essay of 1911 is one of the first based on reasonably extensive use of Ehrlich's famous '606.' It gives an excellent picture of the early methods of arsphenamine treatment, and contains many ideas of a most experienced clinician that are still of value for practising syphilologists. Its lucid style makes it very good reading. Francis Tomlinson Gardner's bibliography and delightful biographical sketch of the great German scientist from Breslau, the memory of whom the Nazis have tried in vain to obliterate, add considerably to the value of the excellent little volume.

ERWIN H. ACKERKNECHT

* * *

THE ABORTION PROBLEM. *Proceedings of the Conference Held Under the Auspices of the National Committee on Maternal Health, Inc., at the New York Academy of Medicine, June 19th and 20th, 1942.*

Howard C. Taylor, Jr., Conference Chairman. Published for the National Committee on Maternal Health Inc., by The Williams Wilkins & Company, Baltimore. $3.50. xii + 182 pp. 1944.

Except for three papers which were omitted, either at the request of the author or for the purpose of earlier publication, this volume represents the Proceedings of the Conference on Abortion Problems, sponsored by the National Committee on Maternal Health, which was held in New York City on June 19 and 20, 1942. Some 50 prominent members of the medical, legal, and teaching professions were in attendance for the purpose of discussing the general problem of human abortion under the following headings: (1) The Magnitude of the Abortion Problem; (2) Spontaneous Abortion and its Prevention; (3) Social, Moral, and Economic Causes and Control of Abortion; and (4) The Control of the Abortion Problem.

The discussions relative to the magnitude of the abortion problem were unanimous in their consensus that it is truly enormous in America. This can be more easily grasped when it is realized that some 30 per cent of all maternal mortality follows abortion.

The problem of spontaneous abortion as related to embryology, endocrinology, and serology is apparently being handled very satisfactorily as a result of fruitful physiological research. The social, legal, and medical aspects of criminal abortion are extremely complicated and difficult to analyse; hence, the utter failure to date in attempting to curb this dangerous, yet lucrative practice. Basic educational and religious training concerning the value of human life and the use of contraceptives, as well as the social stigma attached to the phenomenon of giving birth to an illegitimate child, are all tremendous forces acting either for or against the inception and subsequent attempt to terminate an unwanted pregnancy.

In the matter of controlling criminal abortions, a number of cogent suggestions have been presented, namely: (1) better legislation, not only for the purpose of outlawing the criminal abortionist, but also for protecting the honest practitioner in cases where surgical abortion is indicated; (2) improved group medical insurance, to cover not only the hospitalization of maternity cases, but pre- and post-natal care as well; (3) a system of pregnancy registration and public health control, just as in the case of epidemic or contagious diseases; (4) a complete system of education in the physiology of sex and reproduction, the use of contraceptives, and the dangers of abortion, to be carried out in the public schools, pre-marital clinics, hospitals, and general practitioners' offices; and finally (5), since the criminal abortion problem maintains itself almost entirely on public ignorance and official indifference, the fundamental method of bringing it out into the open where it can be made a topic for open discussion and action, similar to the manner in which the syphilis problem was forced upon the public mind some five or six years ago.

These papers are as refreshing as they are enlightening, and will undoubtedly be read with much interest, not only by the medical profession, but by all social, legal, and research workers interested in the problem of human abortion. There is an index to the volume.

B. AUBREY SCHNEIDER

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WOMAN'S MEDICAL PROBLEMS.

By Maxine Davis. Whittlesey House, McGraw-Hill Company, New York and London. $2.00. xv + 220 pp. 1945.

While one might assume that the natural adviser on medical problems should be a physician, there are few medical men who could have done as good a job with the subject matter of the book under review as has its author, a laywoman. Besides a natural gift for and a long training in popular writing on health matters, she has obviously familiarized herself very thoroughly with the various topics which she discusses in her book. They are presented soundly and readably, with no suggestion of De Kruiffian sensationalism.

Eighteen chapters make up the volume, dealing with such subjects as menstruation, pregnancy, abortion, childbirth, sterility, cancer, etc. The fact that much of the material has been previously published in Good

Housekeeping magazine does not detract from its value. Miss Davis studiously avoids including any suggestions as to treatment, and even a very critical medical reader will find little to criticize from the standpoint of scientific accuracy. The Foreword is by Dr. Fred Adair.

A few minor flaws may be noted. For example, in discussing uterine bleeding she emphatically states: "Never let a doctor use radium." She can scarcely mean this, for practically all gynecologists consider that one of the most important of all indications for the use of radium or x-ray is in the cure of the very common functional bleedings in women approaching the menopausal epoch. Again, she obviously confuses stem pessaries (for cervical insertion) and the vaginal pessaries used in the management of displacements. In the chapter devoted to Caesarean section she uses the spelling Caesarian throughout, and this is not in conformity with either usage or dictionaries.

Aside from a few minor flaws of this type, however, the book impresses the reviewer as an excellent one, which women can be expected to read with pleasure and profit, and without any of the apprehensions with which the average reader is apt to approach health literature in general.

EMIL NOVAK

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THE PATHOGENESIS OF TUBERCULOSIS.
By Arnold R. Rich. Charles C. Thomas, Springfield, Ill. and Baltimore. $10.50. xxiv + 1008 pp. 1944.

Aside from being a monumental storehouse of information on all phases of tuberculosis, this book, containing 21 chapters, should be of great interest to the research worker. The author critically analyzes practically all of the 1417 references, utilizing those portions which substantiate his convictions on the phase under discussion. The forceful technic of expression is stimulating to the reader, who soon finds the book pleasant reading matter and himself infected with a similar analytical attitude of mind.

The purpose of the book has been "to present the background for the interpretation of the pathogenesis of the disease, i.e., the factors that determine the character of the lesions, and the progression or arrest of the infection, and the principles that govern the action of those factors."

In the opening chapter, Rich discusses the three types of chemical constituents, protein, carbohydrate, and lipid, which have been isolated from the tubercle bacillus, and notes that while they are undoubtedly responsible for the occurrence of the tissue damage, constitutional symptoms, formation of epithelioid and giant cells, and thus tubercles, nevertheless amounts of each of the isolated fractions far greater than would exist in natural infection must be injected into normal animals in order to produce these effects. He repeatedly states that no constituent of the tubercle bacillus with toxicity for the normal animal probably exists, and yet he points out that with continued purification of the protein it becomes less toxic, which, of course, implies the removal of a toxic fraction. Furthermore, in a later chapter he states that the acute inflammation produced by injecting tubercle bacilli into the normal body varies directly with the number of bacilli introduced, and that this effect cannot be regarded as a non-specific or traumatic effect, since the injection of a corresponding amount of saline does not give a similar effect. The protein becomes a highly active poison in the sensitized tuberculous animal and therefore responsible for necrosis. It must constitute an essential part of the sensitizing agent.

The relationship of the various types of acid-fast bacilli to their pathogenicity for various animals is considered, and on the basis of existing evidence Rich questions the possibility of infection in man with the avian bacillus. Types of tubercle bacilli are differentiated chiefly on the basis of differences in culture and pathogenicity, and the question of alteration of their virulence and morphology are considered. The true nature of virulence is not clearly understood, but it is dependent upon the survival and multiplication of the bacilli in the body.

In the chapter on native resistance in different species and races, there is a very instructive discussion of the difference between childhood and adult types of tuberculosis and its importance in analyzing the well-known differences in resistance which exist between the negro and white races. The various factors, such as heredity, sex, age, dosage of bacilli, repetition of infection, location of lesion, and environmental factors important in individual resistance are discussed at length. Such factors as temperature, oxygen supply, hydrogen-ion concentration, phagocytosis, etc., are important in causing inhibition of the progressive multiplication of tubercle bacilli in the tissues and thus in determining native resistance.

The author attempts to clear up the misconceptions and confusions as to the various types of hypersensitivity. In the anaphylactic or Arthus and pollen type of hypersensitivity, there is specific sensitization of the involuntary muscle, vascular endothelium, and possibly of the glandular epithelial cells of the respiratory tract; and antibody exists in the blood stream and can be passively transferred. On the other hand, in the bacterial or tuberculin type of sensitivity there is a gradual and progressive local appearance of inflammation, and the cells in general are sensitized. Although the attempts of various investigators to demonstrate the presence of sensitizing antibody in this type of sensitivity have met only with irregular success, Rich says that there are persuasive reasons for believing that there is specific antibody and that it is possible that it may be closely associated with the cells instead of being free in the circulation, where it would be available for passive transfer. Desensitization can be effected in all these types of hypersensitivity, and the mechanism and implications of desensitization are discussed.

A certain degree of resistance to the tubercle bacillus can be acquired by previous infection or by vaccination, but this is dependent upon the number and virulence of the bacilli, the route of infection, and the individual constitution. In discussing the role of hypersensitivity in acquired resistance, Rich concludes that "one should certainly avoid both the view that hypersensitivity is always deleterious, and the view that it is always essential for the successful operation of acquired resistance." While it has not been demonstrated that antibodies play an important role in acquired resistance, it is probable that they do. With acquired resistance there is also a lymphocytosis, and the bacilli do not survive as well in the mononuclear phagocytes. Many practical factors, such as nutrition, physical and mental overstrain, intercurrent infections, trauma, occupation, endocrine disturbances, alcoholism, and climate have an important influence on resistance. Dosage of tubercle bacilli and frequency of infection also are important. Rich does not find the available evidence sufficient to believe that an occupational hazard exists for doctors, medical students, or nurses.

The factors concerned in the formation of epithelioid cells, giant cells, tubercles, inflammation, necrosis, caseation and softening, the symptoms in tuberculosis, and those factors responsible for the differences in children and adults, as well as the reason for the apical site of adult type pulmonary tuberculosis are considered. Both endogenous and exogenous reinfection occur, but it still is not known which is more common. Familiar types of lesions are presented and there are many beautiful illustrations of the pathological effects of tuberculosis throughout the book.

The concluding chapter shows that the mortality rate from tuberculosis has decreased phenomenally during the past 40 years, so that it now holds seventh instead of first place in the list of leading causes of death in the United States. Nevertheless, it is still the most common cause of death in the important age period from 15 to 45. Rich believes the most effective cause for this decline has been the increasing improvement in living conditions.

In such a comprehensive discussion, it is to be regretted that some mention was not made of the changes which occur during the development of tuberculosis in the blood and pleural exudates, such as those affecting the serum proteins, cholesterol, lecithin, and sedimentation. A discussion of amyloidosis would also be welcome.

Some typographical errors exist, but on the whole the book is well published. It is a necessary addition to the library of physician, research worker, and student.

Florence B. Seibert

Penicillin Therapy *including Tyrothricin and other Antibiotic Therapy.*

By John A. Kolmer. D. Appleton-Century Company, New York and London. $5.00. xv + 302 pp. 1945.

The very large literature that has accumulated on the methods of standardization, the properties, dosage, and forms of administration of penicillin makes it desirable to have such a concise text as the present volume for the medical practitioner. The author has succeeded in reviewing and summarizing the important literature on this subject, although no attempt has been made to include all published articles. The medical teacher and biologist will find also in this small volume all the information he may desire concerning the clinical applications of penicillin and tyrothricin.

A general review of the antibiotic drugs is presented. Penicillin production methods and assay technique are described in detail, so that an experienced hospital bacteriologist could conduct assays by following the directions set forth in the text. In accordance with the title, the major portion of the volume is devoted to details of penicillin administration in the clinic. The author has maintained a judicial sense in reviewing the clinical literature, and he has not hesitated to point out over-enthusiastic reports. A complete bibliography is given with each of the book's twenty-three chapters.

The usual intramuscular methods of administration of penicillin are described completely. The increasingly popular bone-marrow, or intramedullary type of injection is described, and techniques are diagrammed. New oral administration methods are set forth in the appendix. The clinician will find much of value here.

C. J. Carr

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Yellow Magic. *The Story of Penicillin.*

By J. D. Ratcliff. Random House, New York. $2.00. xv + 173 pp. 1945.

From its beginning—"I have no doubt that many people will quarrel with the title of this book"—to its last words, those of Fleming himself: "People have called penicillin a miracle. For once in my life as a scientist, I agree. It is a miracle which will save lives by the thousand"—this book is good reading, a worthy example of popular science at its best. Not only the early work of Fleming on *Penicillium notatum* and the labors of Florey, Chain, and their coworkers here find a fitting memorial. The opening of the entire field of chemotherapy through the work of Ehrlich, the later herculean efforts of Domagk ending in the discovery of prontosil and the sulfa drugs, and the pioneering efforts of Dubos of the Rockefeller Institute to find and extract a germ-killer from soil bacteria are also recounted and place the current story of penicillin in its appropriate setting. The story of mass *Penicillium* culture and penicillin production in America during the war is dramatic. The story of the clinical testing of penicillin in cases of wounds, burns, and gas gangrene, staph infections, meningitis, gonorrhea, osteomyelitis, bacterial endocarditis and syphilis and other diseases cannot fail to stir the spirit. Only once in a great while does the narrative run away from the author, as when he talks of "colonies" of pneumococci in the blood, or colonies of staphs "looking feeble."

In most respects, too, the account seems well balanced and not given to over-exaggeration. Only in regard to the mutability of organisms to resistant forms is too little said. The mutability of *Penicillium* itself is regarded as environmental modification rather than genetic change. Perhaps penicillin's entire non-toxicity is not left sufficiently open to question. These are very minor flaws. By and large, few such admirable books have been written about science for the average layman. The book includes excellent photographs, illustrations, and a useful index, unusual in a book of this sort.

Bentley Glass

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The Story of Penicillin.

By Boris Sokoloff. Ziff-Davis Publishing Company, Chicago and New York. $2.00. 167 pp. 1945.

The story of penicillin is here told briefly in non-technical style. The first chapter introduces the reader to Metchnikoff and Metalnikoff, and to the accumulation of evidence of antibiosis even in the early days of bacteriology. The discovery of penicillin is then described, and the development and experimentation with the drug in England. Under the title "Cinderella of Science," problems of production are discussed, the role of para-amino benzoic acid is presented and also the therapeutic action of penicillin B and proflavin. The use of penicillin is described mainly by presentation of case histories. The fifth chapter is devoted to other "wonderful tiny chemist-molds" and some of the substances derived from them. The use of moldy bread for wound dressings among European peasants is mentioned. The concluding chapter emphasizes the continuity of ideas in scientific research.

Unfortunately the text does not progress very smoothly. At times the reader is apt to be confused by the author's detours. A more straightforward and sober presentation would be desired by most people. More facts as to why penicillin is a "wonder drug" could have been included. On the subject of Pasteur versus Ehrlich, some scientists might well take issue.

Appended to the text are 13 pages of footnotes, an extensive bibliography for a book of this type, and an index. There are no illustrations.

Harriette Vera

Fundamentals of Pharmacology.

By Clinton H. Thienes. Paul B. Hoeber, Medical Book Department of Harper and Bros., New York and London. $5.75. xviii + 497 pp. 1945.

This book is intended to present the aspects of pharmacology which are essential to a medical student and to refresh the knowledge of the practitioner.

The source, chemical nature, preparation, dose, absorption, distribution, fate, excretion, and actions of each drug as determined experimentally are emphasized.

The material is arranged according to the site of action of the drug (central nervous system, peripheral nervous system, muscles, diuretics); the antiparasitics; the hormones, special minerals, and tissue extracts; vitamins; drugs which act on body surfaces; chemical diagnostic agents; actions of drugs on cells; and pharmacy and prescription writing.

The material is presented in a clear and well organized manner and should be a valuable text for the medical student. Since the scope is limited, it is probable that most biologists would find a general reference book more useful.

William E. Evans, Jr.

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Alcohol Hygiene. *Vol. 1, No. 1. September–October, 1944.*

Published bi-monthly for The National Committee on Alcohol Hygiene, Inc.; by Alcoholism Publications, Baltimore. Free upon request.

The stated purpose of this bimonthly bulletin of short papers and abstracts by medically or psychiatrically trained workers is "to disseminate scientific information to the public through various *educators* on the subject of alcoholism with the primary view of *educating* individuals and the community about alcoholism . . . and the significance of this medical psychiatric problem in its effects on, and relation to, both the individual and the community."

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PSYCHOLOGY AND ANIMAL BEHAVIOR

The Psychology of Women: A Psychoanalytic Interpretation. *Volume Two—Motherhood.*

By Helene Deutsch. Grune and Stratton, New York. $5.00. vi + 498 pp. 1945.

In this second volume, the author draws to a conclusion her views concerning the psychological life of normal women in our society. Because the treatment is of the normal woman, only passing use is made of pathological material. The volume is concerned essentially with the psychological and physiological aspects of motherhood in their combination as a psychosomatic problem. Every aspect of motherhood is discussed, and the author's deep understanding of motherliness and of the strict sexual aspects of motherhood are noteworthy. In dealing with the psychology of the sexual act, she discusses some aspects of sexual intercourse which are not generally understood even by experienced psychiatrists. She discusses the psychogenic influences of sterility and fertility with a sureness which most of us lack. Her contributions in this field are important even if they lack substantial proof. Concerning pregnant women she makes the interesting statement that "to a striking degree most intuitive and introspective women shy away from observing their own psychic processes during pregnancy. One might almost say they are deliberately trying not to observe them. This profound motivated behavior is one of the reasons why we have so little information about the psychic life of pregnant women." In spite of this paucity of material, the author gives a remarkable demonstration of her insight into the psychological life, the aspirations, the fears, the imaginations of pregnant women. She quite rightly concludes that the psychological life during pregnancy depends very greatly on the psychological atmosphere at the time of conception. In the chapter on delivery she makes a rather telling statement, that the use of modern methods to relieve woman of pain with delivery may have distinctly deleterious effects on the mother's psychology. She also observes that death of a child at delivery leaves much less residue of psychological upheaval than does the death of a child later on.

The mother-child relationship is superbly described. There follow chapters on problems of unmarried mothers, adoptive mothers, and stepmothers, showing a very great insight into all three of these special problems. She makes the important point that adoptive mothers have in all principal essentials the same opportunity to achieve psychological consequences from their situation that real mothers have. The principal obstacles confronting adoptive mothers lie in their own psychology. She sums up her reaction to the stepmother problem with the statement, "On the whole it can be said that a good mother is also a good stepmother, and so much of this difficult problem can be left to her maternal feelings." A final chapter on the climacterium is notable for the author's insistence that in the climacterium there is a resurgence of the same problems which had first appeared in adolescence. She goes so far as to say that knowing the problems of adolescence in any patient gives her a feeling of safety in prognosticating the course the climacterium will take.

Helene Deutsch would certainly merit inclusion in that group of well-rounded individuals whom the Germans used to call "Menschenkenner," and which I am assured by a psychoanalytic colleague is practically extinct at this time. I am unaware of any other book that begins to cover the subject of Helene Deutsch's choice in such comprehensive fashion. She has observed and recorded her impressions on every variety of woman in every stage of woman's life, with only one exception as far as I can note. She makes no reference to that growing list of women who have achieved motherhood by artificial insemination. Probably she has also observations on these women, but not enough as yet to justify inclusion in a book. She touches upon dramatic portrayals of feminine psychology from belles lettres in this second volume in a fashion much less annoying to this reviewer than in the first volume. Here it is but a casual touch, whereas in the first volume the material seemed to be used for the demonstration of psychological theories in a way that does violence to scientific method.

It is impossible to do justice to such a pair of volumes in any review. One has to read to believe the wealth of observation and understanding, and the helpfulness even of those theories which may seem from time to time to outstrip established fact. This is the second of two volumes which must not be missed by any psychiatrist. All will look forward eagerly to the two additional promised volumes, one on the pathologic manifestations of the psychology of women, and the other on the contribution of cultural and social factors to feminine psychology.

WENDELL MUNCIE

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THE HUMAN MIND. *Third Edition, corrected, enlarged, and rewritten.*

By Karl A. Menninger. Alfred A. Knopf, New York. $5.00. xvii + 517 pp. 1945.

To the fourth edition of this excellent introduction to the principles of psychiatry there have been added a section on new developments in therapy and a comprehensive bibliography, arranged by topics corresponding to the organization of the text. The discussion of new therapeutic methods is relatively brief, and there is still only a bare mention of the advances in the knowledge and treatment of military psychiatry made during World War II.

The author's position on the significance of hereditary factors in the determination of neuropathic constitution and mental disease will not satisfy geneticists. He not only seems to follow the general tendency of medical men to think of heredity solely in terms of an unbroken transmission of traits from generation to generation, but quotes with evident approval such nonsense as the statement that "we can *define* environmental forces as those over which we have potential control, and hereditary forces as those over which we have as yet no possibility of control." This means, no doubt, that because polydactyly can be corrected by surgery, and diabetes mellitus by insulin administration, they thereby cease to be hereditary. He also speaks scathingly of the interpretations of studies of twins. It is certainly true that identical twins as a rule create for themselves a somewhat more similar environment than even same-sexed fraternal twins, but that is hardly sufficient ground for denying any validity to the conclusions as to the significance of genetic similarity. It is noteworthy that the work of Rosanoff in this field is completely ignored.

Biologists who wish to settle in their own minds the question of the balance in modern psychiatry between science, ars medica, psychoanalytic dogma, and unsupported speculation can hardly find a better book for their purpose, or a more authoritative exponent than the author.

BENTLEY GLASS

INVISIBLE ANATOMY. *A Study of 'Nerves', Hysteria and Sex.*

By E. Graham Howe. Faber and Faber, London. 10s. 6d. 333 pp. 1944.

This is a treatment of personality from various aspects, normal and abnormal, following Jungian analytical psychology. The author resorts to diagrams to bring illumination into his thought concerning the structure and workings of personality. They may do just that for him but they fail to accomplish it for the reviewer. On the other hand, Howe's special chapters dealing with various psychopathology pictures, neuroses, sex abnormalities, and peculiar characters of other sorts are masterfully written, and the author has evidently in some cases achieved considerable therapeutic success by the ingenious use of analytical psychological methods. As with any psychiatric presentation, there is a great deal of fundamental and worth-while observation, and as with most such presentations there is a heavy overloading with theory, speculation, and mythology put to the use of theory. Too much importance is attached to all this theoretical speculation, and the actual facts of this small book could be expressed in half the space with no deficit in the reader's understanding.

WENDELL MUNCIE

THE LIFE OF CHILDHOOD. *A Contribution to Analytical Psychology.*

By Michael Fordham. Kegan Paul, Trench, Trubner and Co., London. 15s. viii + 154 pp. 1944.

This book provides an extension of Jung's teachings of analytical psychology to the realm of normal and problem children. The principal differentiation of this material from other varieties of child psychology is the introduction of Jungian archetypes as the symbols necessary to the proper understanding of child psychology. Actually, the observations of children as set forth in this book show nothing different from the observations made by other methods, and the author's painstaking analysis of child problems and his evident therapeutic successes with them point to the usefulness of his type of treatment, besides the other types of treatment, too. An interesting part of the book has to do with children's drawings, and here also the archetypes are introduced as explanation in a manner which leaves me unconvinced, but the ingenuity of the process must be acknowledged. The last chapter on treatment is full of sage advice, sage whether one is a Jungian or an adherent of any other system.

WENDELL MUNCIE

PSYCHOLOGY FOR THE RETURNING SERVICEMAN.

Prepared by a Committee of the National Research Council. Edited by Irvin L. Child and Marjorie Van De Water. Infantry Journal, Washington; Penguin Books, New York. 25 cents (paper). 243 pp. 1945.

The serviceman returning from World War II is faced with a multitude of physical, mental, and social problems and adjustments of such magnitude that the services now recognize, as part of their duty, the necessity for a complete program of general rehabilitation and personnel guidance. This little volume has been prepared by a number of Army and Navy personnel, civilian physicians, psychologists, psychiatrists, and general workers in the fields of recreation, sociology, welfare, and guidance, and is intended primarily for use by the returning serviceman and his family in bridging the gap between his life on the fighting front and life back home.

Although it is apparent that many servicemen have withstood the stresses of regimentation and combat without any noticeable changes in personality or outlook on life, there are others whose experiences in the front lines or in prison camps have left deep-seated mental impressions or serious physical handicaps which interfere with a normal return to life and work at home. In many instances the difficulties are of such a subtle nature that the man is not able to recognize them for himself; hence the need for consulting a psychologist or psychiatrist. In other instances where the difficulties are imposed by the loss of limbs, sight, hearing, etc., the problem of adjustment must be accomplished by the process of learning new skills and techniques in order to begin an entirely new and different type of life than was contemplated before the war.

An enormous amount of sound reason and common sense has been instilled into these eighteen chapters concerning such pertinent subjects as meeting people, finding a job, picking a wife, returning to a family, recovering from mental or physical illness or injury, and in general, taking part in a normal society again.

Although some servicemen will undoubtedly resent the thought that they are considered different, and that they need a little book to help them get adjusted, there are others who will welcome the kindly and helpful words of encouragement and advice offered in these pages.

B. Aubrey Schneider

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Textbook of Abnormal Psychology. *Third Edition.*
By Roy M. Dorcus and G. Wilson Shaffer. The Williams & Wilkins Company, Baltimore. $4.00. xv + 547 pp. 1945.

In this third edition of the authors' well known work on abnormal psychology considerable new material has been added. Recent published research has added some 365 new references. The book follows the form contained in the two previous editions, with chapters on: the field and scope of abnormal psychology; sensory disorders; motor disorders; disorders of association and memory; theories of disorders of the central functions; desires, feelings, and emotions; sleep, dreams, and hypnosis; classification of mental diseases—organic psychoses and epilepsy, functional psychoses, psychoneuroses, mental deficiency and psychopathic personality; treatment by physical and chemical assault; and psychotherapy. There is a bibliography and an index.

The authors give a very well balanced presentation, from both theoretical and practical standpoints, of the current thought concerning abnormal psychology and the treatment of abnormal psychological conditions. There is an absence of any particular bias and also a healthy lack of that kind of enthusiasm for any special method which so often leads to scientific fallacy.

Just what the difference between this text and a textbook of psychiatry may be, it is hard to see. The same material is covered in the ordinary textbook of psychiatry, and it may be that Ross McC. Chapman's foreword calling attention to the fact that he still thinks that it is important for treatment to be in the hands of medically trained personnel constitutes a necessary warning to those psychologists who might from acquaintance with this material presuppose a capacity to handle psychiatric material independent of a physician. This last is clearly not the stand taken by the present authors, however, for they make it plain that a psychologist should never attempt treatment of the patient without the benefit of complete physical examination. It is doubtful whether this is enough, however, because the whole problem of psychosomatic medicine, the effects of emotions on physical functioning, and the revision of this situation presuppose in the treating authority an intimate acquaintanceship with material that is not at the fingertips of psychologists. It may be that close cooperation would accomplish the same ends, and no doubt has accomplished the same ends in plenty of cases.

This is an excellent textbook, showing a grasp of every aspect of the field, bolstered by a great deal of material of a bibliographical sort, and yet so presented as to be quite easily readable. One very desirable feature in the text is the constant endeavor to present the principles of abnormal psychology through the consideration of the normal. The text will be found very useful to students of psychology as well as to medical students, and even to psychiatrists and psychologists with long experience in their fields.

Wendell Muncie

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Crime and the Human Mind.
By David Abrahamsen. Columbia University Press, New York. $3.00. xii + 244 pp. 1944.

This book from the hand of a well-known Norwegian criminologist, now working in this country, gives an excellent statement of present views concerning that subject, particularly concerning the psychological and psychiatric aspects of crime. The theses are illustrated by case histories from the author's own records and from other sources. He seems too optimistic in concluding that psychoanalysis can make any sizable change in certain psychopathic states. This seems to be his stock recommendation. Yet the book is an excellent statement of the general subject and the present status of criminology.

Wendell Muncie

* * *

HUMAN BIOLOGY

The Aleutian and Commander Islands and Their Inhabitants.
By Aleš Hrdlička. The Wistar Institute of Anatomy and Biology, Philadelphia. $5.00. xx + 630 pp. 1945.

In this posthumous publication the author has recorded his experiences and anthropological work during three summers (1936 to 1938) on the chain of islands bordering the Behring Sea. The introductory section of this monograph presents brief general and historical notes in regard to the Aleutian Islands. In a large second part (186 pages), all available ethnographical data on the Aleuts have been compiled and abstracted from widely scattered literature. This orderly collection of more or less fragmentary information preserves a picture, though quite incomplete, of the customs, clothes, food, habits, etc., of the Aleutian natives as found by earlier explorers.

The third part (186 pages) describes the author's trips and surveys in the islands, recounting the daily happenings on the basis of field-diaries. These simple notes supply random information on the weather, transportation, food, etc., on these barren islands and enumerate the findings of the remains of the aboriginals and their work in the ground or in caves. This section includes much irrelevant, repetitious, and quite personal detail which does not fit too well in the frame of an otherwise technical, scholarly volume.

A fourth part (83 pages) is devoted to the archeological objects from the Aleutian Islands, placing them on record in a purely descriptive manner, and without going into comparative aspects. In the final, fifth part (98 pages) the human skeletal remains, successfully collected in adequate series, are thoroughly catalogued with the most essential measurements and systematically compared with corresponding data for other human groups.

These interesting discoveries and analyses are summarized in part as follows:

> "All the habitable islands in the Aleutian archipelago, barring the Commanders, had once been occupied by man; and man had multiplied there until he had to utilize every spot fit for human habitation.... The skeletal remains recovered from all older sites, and to some extent also the cultural objects, have shown clearly that the Aleutians had in the course of time been occupied by two physically and also otherwise distinct strains of people, the Aleut and before them the 'pre-Aleut'....There was found not the slightest indication that there might have been even older inhabitants of the islands than the pre-Aleuts. The advent of the latter may, it seems, be referred to the earlier part of the Christian era, but not before this. The coming of the Aleuts, which according to many indications was a gradual spread from the Peninsula westward, could not have taken place more than a few centuries before the coming of the Russians. They met the older population in the islands, replaced it, probably by force, in the more eastern parts of the archipelago, and then spread thinly westward, admixing there with what remained of the older people. The Commander Islands, it is now positive, were never peopled before the advent of the Russians."
>
> "Somatically, the pre-Aleuts differed very considerably from the Aleuts. They were larger people, oblong-headed, and with various other skeletal differences....Neither the pre-Aleut nor the Aleut were Eskimo, or even nearly related physically to the latter. In their cranial characters the pre-Aleuts resembled closely the Siouan Indian, while the Aleuts were very close to one type of the Siberian Tungus."

With these ably supported conclusions this monograph contributes a significant chapter to the prehistory of the New World.

The volume ends with three short appendices (two dealing with ethnographical matters and one with associated animal remains), with a valuable bibliography, and an all-too-condensed index. This monograph has been printed by the Wistar Institute in a perfect fashion, including the reproduction of the 239 illustrations.

A. H. SCHULTZ

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A SUMMARY OF YUKI CULTURE. *Anthropological Records, Volume 5, No. 3.*

By George M. Foster. University of California Press, Berkeley and Los Angeles. $1.00 (paper). Pp. iv + 155–244 + 1 map. 1944.

Basing his treatment on information obtained in 1937 from the few survivors of the Yuki, a North Central Californian tribe, the author has tried to make as full a reconstruction as possible of the old material and spiritual culture. The material culture of these warlike hunters was poor; their religion is remarkable in several respects, particularly through the belief in a High God. Of special interest in this valuable little monograph are the materials on Yuki medicine and on religion, including the Pentecostal movement. The absence of any information on the forms of shelter is surprising.

ERWIN H. ACKERKNECHT

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ONE AMERICA: *The History, Contributions, and Present Problems of Our Racial and National Minorities. Revised Edition.*

Edited by Francis J. Brown and Joseph Slabey Roucek. Prentice-Hall, New York. $3.75. xvi + 717 pp. 1945.

This is a thoroughly revised edition of the earlier book, *Our Racial and National Minorities.* Thirty-five contributors endeavor to give a short historical view of the forty-three "minorities" of which this nation is composed, of their organizations, press, and cultural contributions. While the organizational data provided are in general adequate, the treatment of the cultural contributions is often much less satisfactory. A second part of the book consists of twenty-three sometimes excellent general essays on the foreign language and negro press and radio broadcasts, on national minorities in foreign and domestic politics, on the education and religion of the foreign born, etc. A final group of essays undertakes to develop a program of cultural democracy in the U. S. The volume contains no contribution whatsoever that deals with the many biological and pseudobiological aspects of the minority problem.

The intentions of the book are most commendable. A scholarly level is in general maintained (though to find, e.g., on p. 97 of a *revised* edition the Sieur Cavalier de LaSalle and the trader Joliet characterized as "fathers" and "missionaries" is somewhat painful). The book includes an enormous amount of valuable information in a relatively limited space for ready reference. In an extensive bibliography the interested student will find an excellent tool for further research upon special problems.

ERWIN H. ACKERKNECHT

* * *

ANGEL IN THE FOREST. *A Fairy Tale of Two Utopias.*

By Margaret Young. Reynal and Hitchcock, New York. $3.00. 313 pp. 1945.

The story of New Harmony has been told many times, but it bears retelling. Such a significant chapter in the history of the development of American scientific thought deserves a better fate than the neglect which has too often been its fate; consequently every new contribution is to be welcomed. But the work here under review must be considered a failure, in so far as contributing anything new is concerned.

This book is hard to classify. It is not factual history, whose function is to tell the truth and nothing but the truth; nor is it philosophical history, whose function is to interpret the truth; nor is it epic history, whose function is to allegorize the truth. According to the blurb it is "history-fable," and the function of history-fable, if one is to judge by this example, seems to be to do violence to the truth. Consider, for instance, the brief biographical sketch of Charles Alexander LeSueur.

According to the author, LeSueur was a member of the ill-starred expedition led by La Perouse, and escaped the disaster which overtook that expedition by remaining at Botany Bay to collect natural history material. After weeks, months, and finally years had passed, LeSueur was rescued very much against his will by the crew of an English vessel, who forcibly abducted him, only to put him ashore at the first port of call when they learned who he was. This happened to be in the West Indies, where he met William Maclure, who was recruiting settlers for Robert Owen's cooperative colony at New Harmony.

But La Perouse was wrecked in 1788, and New Harmony was founded in 1824. To the reviewer it does not seem reasonable that LeSueur should have waited all that time for the return of his companions without having any suspicion of the disaster that overtook them, nor that the first port of call of a vessel leaving Australia should have been in the West Indies. As a matter of fact, however, LeSueur was only seven years old when La Perouse sailed from France, and it is inconceivable that he could have accompanied the expedition. Furthermore, his name does not appear on the roster of personnel which was among the documents that La Perouse sent back to Paris from Petropavlovsk by De Lesseps. Later, in 1804, LeSueur did go to Australia with the Baudin expedition, as an artist and not as a scientist; but in 1805 he was back in France, having returned safely with Baudin. In 1809 he was exploring the surface waters of the Mediterranean with his towing net, and in 1815 he was in Philadelphia publishing the results of this investigation. That Maclure met LeSueur while recruiting for Owen is extremely unlikely; for Maclure did not become acquainted with Owen until 1824, when he had already been president of the Academy of Natural Sciences for seven years, an organization of which LeSueur was a staff member.

This is perhaps the most flagrant historical inaccuracy in the book, but there are many similar ones of a minor nature; for example, the misspelling of such a well-known name as that of Rafinesque. Another is the statement that Maclure died in Mexico City. The Mexican capital, like our own, is not in the state of the same name, but in the Federal District. Maclure died in the state (but not in the city) of Mexico. The author states that Madame Fretageot was with him when he died, that she died a few days later, that both obituaries were published in the same issue of the New Harmony Disseminator, and that Say died later in the same year. But Weiss and Ziegler, in their biography of Say, put his death in 1834, and those of Madame Fretageot and Maclure in 1833 and 1840, respectively. Further comment appears unnecessary.

The author's statement that celibacy was one of the religious tenets of the Rappites is also open to question. The Rappites were celibates, it is true, but on economic rather than religious grounds. Probably every persecuted minority in eighteenth century Germany was represented among them, but none were required to give up their religious beliefs. They were asked only to be tolerant of each other. There was no unity among them except the unity of mutual respect. It stands to reason that no woman can be an efficient agricultural laborer while carrying a child, and in a community composed of recruits from a nation where it was an ancient tradition that the heavy labor in the field be performed by women, it was not unnatural that they should rebel against being required to function as breeding machines as well. When it became evident that the influx of new members that were arriving from the fatherland on every Ohio river steamer would more than suffice to maintain the population, Rapp began to urge the practice of celibacy, but he continued to perform marriage ceremonies both within and without the colony. On one or two occasions he rebuked parents who brought more children into the world than they could care for, but as he did not discipline the offenders, the statement made by the author that he murdered his own son because the latter's wife was about to bear him a child seems highly improbable.

Throughout the work the author takes a morbid delight in repeating scandal that cannot be verified. The story of the death of young Rapp is only one instance of this. Anothr is the statement that the corpse of a red-haired woman was found in the coffin of Thomas Say when it was removed from the cemetery to the Maclure family vault. The author admits that this story cannot be authenticated. Why then was it repeated? Again, she states that the Quakers sent a shipload of maize to Ireland to alleviate the famine of the 1840's, which failed of this purpose because the Irish didn't know how to prepare corn for eating. It is well known, however, that the Quaker relief ship was laden, not with corn, but with potatoes, with which the Irish were indeed familiar.

The author also tells us that Robert Dale Owen in his old age became both a pacifist and a drunkard. Whether he ever became either one the reviewer is unable to state, but it is inconceivable that he could have become both, for pacifism and inebriety hardly go together. Strength of character is a necessary prerequisite for the former, while the latter is the result of weakness of character. The author's treatment of the letter in which Robert Dale Owen urged Abraham Lincoln to sign the emancipation proclamation is very unsatisfactory. She quotes first Owen, "an imperishable name . . . is within your reach," and then Lincoln, "it thrilled me like a trumpet call." The implication is that the appeal to Lincoln's vanity caused him to sign for his own personal aggrandizement. But Owen's letter was actually a carefully phrased document of several pages, the kind of letter that no president except Lincoln would have had the patience to read, and he explained specifically to Stanton that his desk was covered with letters on the subject, but that those who opposed emancipation did so to safeguard the funds which they had invested in enterprises employing slave labor, while those who favored it did so because they had interests in competing concerns. Robert Dale Owen alone was disinterested, and Lincoln was thrilled because there was at least one person in addition to himself who looked on emancipation not as a matter of expediency, but as one of right and wrong. The author's statements are quite correct, but by picking out a pair of brief and disconnected texts and placing them in juxtaposition she has succeeded in creating a false impression. Also, her comparison of the angel Moroni with an octopus is not only scientifically false but is so nauseating in its coarseness and vulgarity that the reviewer refrains from quoting it.

While speaking of angels, perhaps a few words about Gabriel, who suggested the title for the book, may not be amiss. The archangel is said to have descended on New Harmony to give instructions to Rapp, but no one saw Gabriel but Rapp himself, who produced as evidence the stone on which the archangel stood and which bore the impressions of his feet. The author admits that the stone shows signs of recent recutting. If this is the case, why is it not possible that the entire story dates from a later day than that of the Rappite ascendency? This is the theory advanced by John S. Duss, but he was a Rappite himself and therefore prejudiced. However, if the story really was the fabrication of George Rapp, it seems very strange that he should have left the stone behind when he removed the chosen people from Harmony to Economy. The fact that he took a collection of minerals and other natural curiosities with him, which were subsequently deposited in the museum of the University of Pittsburgh, makes it all the more improbable that he should have left the angel's footprints behind.

One naturally wonders what the author's object may have been in producing a book that departs so far from historical accuracy and common decency. The reviewer can throw no light on this question. That historical accuracy was not her aim is evidenced by the absence of any kind of documentation, bibliography, or index. She is a poet, and her attitude to history is essentially that of an operatic librettist toward his subject. But the reviewer, who has long cherished the ambition some day to visit New Harmony himself, to stand beside the monument erected by Alexander Maclure in memory of Thomas Say, and to see the golden rain trees in bloom, wishes that Marguerite Young could have found some other vehicle for the display of her artistic talent.

* * *

ADOLESCENTS IN WARTIME. *The Annals, Volume 236, November 1944.*

Edited by James H. S. Bossard and Eleanor S. Boll. American Academy of Political and Social Science, Philadelphia. $2.50 (cloth), $2.00 (paper); to members $1.50 (cloth), $1.00 (paper). vii + 233 pp. 1944.

This number of the Annals comprises some twenty publications centering around the following general headings: background; social and family setting; wartime employment; health and hygiene; and selected problems. These articles are uniformly good, stimulating, provocative, and thoughtful. Because of this, singling out any special article can only reflect the reviewer's interests. From this standpoint James S. Plant's "Social Significance of War Impact on Adolescents," "Family Backgrounds of Wartime Adolescents" by James H. S. Bossard, "Mental Hygiene Problems of the Adolescent Period" by Dorothy Hankins, "Wartime Recreation for Adolescents" by Roy Sorenson, "Youth and Religion" by Paul Weaver, "Youth and Government" by Katherine F. Lenroot are most welcome, but the whole volume is an important contribution toward understanding this very difficult period in the lives of adolescents. The volume contains also numerous book reviews, seriously and studiously well done.

WENDELL MUNCIE

* * *

DELINQUENCY AND THE COMMUNITY IN WARTIME. *1943 Yearbook, National Probation Association.*

Edited by Marjorie Bell. National Probation Association, New York. $1.75 (cloth); $1.25 (paper). 307 pp. 1944.

These papers presented at the annual and other meetings of the association deal with delinquency in wartime. The important sections deal with: crime and the community; wartime changes in parole and probation; the federal wartime protective program; the war and juvenile delinquency; delinquency prevention movements; community care of delinquent children; psychiatric studies, juvenile and adult; and legal digest.

Donald R. Taft's "American Culture and the Treatment of the Offender," Whitcomb H. Allen's "Young Camp Followers," and Basil L. Q. Henriques' "The Wartime Delinquent in England" are especially interesting. The papers are uniformly good.

Wendell Muncie

* * *

Cooperation in Crime Control. *1944 Yearbook, National Probation Association.*

Edited by Marjorie Bell. National Probation Association, New York. $1.75 (cloth); $1.25 (paper). 320 pp. 1945.

This is an excellent compilation of papers given at the annual meeting and other meetings of the association, dealing with juvenile delinquency especially in wartime. There are seven important parts: the juvenile court and its community relationships; understanding the delinquent; protection and preventive services; community responsibility for the wartime delinquent; parole and the institution; special problems of the adult offender; legal digest.

Dean Roscoe Pound's "The Juvenile Court and the Law" sets the tone for the volume. It is a scholarly treatise on the position of the juvenile court in actual legal practice. Judge Alexander's "Speaking as One Judge to Another" is a frank statement of the vicissitudes of the juvenile court judge. The articles are uniformly good, provocative, and helpful.

Wendell Muncie

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The Dynamics of Culture Change. *An Inquiry into Race Relations in Africa.*

By Bronislaw Malinowski. Edited by Phyllis M. Kaberry. Yale University Press, New Haven; Humphrey Milford, Oxford University Press, London. $2.50. xiv + 171 pp. 1945

This is the third posthumous book of the late Bronislaw Malinowski. It is to be hoped that he will not outdo the record of his English colleague, W. H. R. Rivers, whose executor, G. E. Smith, brought out six volumes of material which Rivers had preferred not to publish during his lifetime.

In the *Dynamics of Culture Change*, Phyllis M. Kaberry has collected from Malinowski's old papers and manuscripts his opinions on a problem which by American anthropologists is generally called acculturation. Malinowski took his practical examples from British possessions in Africa, where he had studied the question. The first part of the book deals with theoretical and methodological aspects. Excellent remarks on what is essential in such studies are coupled with quite superfluous onslaughts upon the historical approach, marked by the other less agreeable characteristics of Malinowski's theoretical writings—his inconsistency, repetitiousness, and somewhat adolescent eagerness to sell his great method. The second, and more original part of the book deals with special problems such as witchcraft, diet, land tenure, and indirect rule among the African natives subject to rapid acculturation.

The shortcomings of the book are partly conditioned by objective factors. The author makes the commendable attempt to implement scientifically a compromise in a situation which, even in the most tactful description, is somewhat embarrassing.

Malinowski, with all his faults, was probably the greatest anthropologist of his generation, and even this posthumous book is therefore quite readable. Yet in my opinion a better contribution of Malinowski to the problems of acculturation and applied anthropology has been made through his numerous pupils who have done quite outstanding work in this special field.

Erwin H. Ackerknecht

* * *

A Comparative Dictionary of the Tahitian Language. *Tahitian-English with an English-Tahitian Finding List. Special Publication Number Six.*

By Edmund Andrews and Irene D. Andrews. The Chicago Academy of Sciences, Chicago. $5.00 (paper). xvi + 253 pp. 1944.

* * *

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

The Autobiography of Science.

Edited by Forest Ray Moulton and Justus J. Schifferes. Doubleday, Doran and Co., Garden City, New York. $4.00. xxxi + 666 pp. 1945.

This is an anthology of original writing, from the Greeks to modern times, selected as outstanding contributions to the different fields of science.

Such a collection naturally cannot include everything; and perhaps it would be carping to complain that biochemistry does not receive a place, or that among the botanical excerpts no mention is made of the most important of plant processes, photosynthesis. Some of the work of Emil Fischer on proteins, for instance, and Priestley's paper to the Royal Society on the purification of air by plants might perhaps find a place here.

Yet, given the difficulty of selection, it must be granted that the book covers a very wide range and gives an impressive picture of the history of science in an eminently readable form. Not the least advantage of this form is the prominence it often gives to the scientific methods and experiments themselves, which tend to be buried in the condensed survey that constitutes the more conventional history of science.

Eileen Sutton Gersh

◆

South America Called Them. *Explorations of the Great Naturalists La Condamine, Humboldt, Darwin, Spruce.*

By Victor Wolfgang von Hagen. Alfred A. Knopf, New York. xii + 311 + ix pp.; 27 plates. 1945.

This is a book for the young fry and for oldsters, too, for those with scientific training and also for those who haven't any. The accounts of the explorations, during a century and a half, of four great naturalists in South America make inspiring and exciting reading. Science and history and human relations are mingled in nice proportions.

There are Charles-Marie de la Condamine and the South American Pedro Maldonado carrying out their triangulations in the high Andes to determine the shape and size of the earth; the Quiteños suspected them of seeking Inca treasure, for otherwise they could only be lunatics. There are Alexander von Humboldt, seeking with Aimé Bonplant for the communication of the waters of the Amazon and Orinoco, and Charles Darwin wandering through Argentina and observing the Fuegians and the Galápagos reptiles. The fourth explorer is Richard Spruce, who for years collected on the Amazon, who watched the rubber boom come to Brazil and who gathered the seeds of the cinchona tree for transportation to India to be grown for quinine, thus transplanting an industry.

◆

Science Year Book of 1945.

Edited by John D. Ratcliff. Doubleday, Doran and Co., Garden City, New York. $2.50. xxviii + 224 pp. 1945.

Like previous volumes of this series, the *Science Year Book of 1945* presents a broad and readable coverage of current science. The introduction is again better than most, if not all, of the articles the editor has chosen from popular journals and magazines. The chemistry of natural gas and its products, and antibiotics in general are here added to piece out the survey. Part I of the book deals with advances in medicine. Part II covers physics and chemistry; Part III, aviation; and Part IV, other sciences. Except for an article on animal migration in the last section, the treatment of subjects of biological interest is thus largely concentrated in the first section. Here one finds no little diversity in quality of presentation, as well as in subject: Penicillin, blood fractionation, the study of pain, the use of tantalum in surgery, corneal transplants, the liver, the skin, children's diseases, mental disease, and fatigue. Two articles on DDT and one on the use of the electronic tube in medicine, from the following section, add to the variety. Most biologists will find this light volume pleasant and informative reading, particularly so in covering those fields of science less familiar to them.

Bentley Glass

◆

The Quest of American Life. *University of Colorado Studies Series B. Studies in the Humanities, Volume 2, Number 3.*

By George Norlin. University of Colorado, Boulder. 2.00. xvi + 280 pp. 1945.

This work is an interpretation of the lives of some of the more important contributors to liberal thought in the United States. The author calls it a study in humanism, an unfortunate choice of label, since this term has been applied in turn to practically every school of philosophic thought since the renascence of learning, and to some which preceded it. In fact, the author tells us that he is giving the word a new meaning, and seemingly proceeds to apply the label humanist to all those characters he admires, somewhat loosely, regardless of how little they may have in common; otherwise it would be difficult to explain the presence of the gentle and saintly John Woolman in the same category as Theodore Roosevelt, who believed that the end justifies the means, and who carried the big stick.

The aim of the author has been, not to write history, but to interpret personality, and in this he has been eminently successful. His enthusiasm for Roger Williams does not blind him to the fact that Governor John Winthrop and Pastor John Cotton, who were responsible for the expulsion of Williams from Massachusetts, were themselves upright men of good character, who were actuated by the purest motives to do what seemed best for the colony.

Roger Williams has never had a biographer. We do not even know what he looked like. What we know of him comes from a multitude of unrelated sources. He is the most celebrated forgotten man in the history of liberalism in the United States. Yet it was this shadowy figure who laid the foundation on which William Penn erected the Treaty of Shackamaxen, Thomas Jefferson the Declaration of Independence, and Abraham Lincoln the Emancipation Proclamation.

The biographers of Franklin, on the other hand, have been legion, and it is therefore surprising that the author has found so much about him that is new, placing his emphasis on the way in which and the extent to which Franklin's personality was molded by the environment in which he developed. Perhaps this is a truer appraisal of the versatile Philadelphian than most.

In a most interesting chapter, the author rescues Hector St. Jean de Crèvecoeur from undeserved oblivion. The collection of letters which this obscure

Pennsylvania farmer wrote to a friend in England gives us a more authentic and more detailed picture of American frontier life in the eighteenth century than any other. The author has devoted more space to Crèvecoeur than to any other figure in his book, and has quoted from him more extensively. He deserves this attention.

On the whole, the author's treatment of the nineteenth century is not so happy as that of the eighteenth. This is to be expected. We are still too close to Whittier, Emerson, and Whitman to appraise them properly, and so much has been written about Lincoln that it is practically impossible to say anything about him that has not appeared in print elsewhere. But why was Robert G. Ingersoll omitted entirely and Robert M. LaFollette dismissed with one brief sentence?

The final chapter deals with the elder Roosevelt, and it constitutes something of an anti-climax. It is as yet too soon to decide whether Roosevelt the humanitarian or Roosevelt the imperialist will be remembered by posterity.

In such a work as this there are bound to be some minor flaws. But the omission of the part played by the American women in the development of liberalism is indeed a serious defect.

Approved Laboratory Technic. *Clinical Pathological, Bacteriological, Mycological, Virological, Parasitological, Serological, Biochemical and Histological. Fourth Edition.*

By John A. Kolmer and Fred Boerner. D. Appleton-Century Co., New York and London. $10.00. lxii + 1017 pp. 1945.

This edition has been extensively revised and much new material has been added. New sections on the examination of blood, feces, and tissues for animal parasites, on methods for examination of the saliva, pancreas function tests, examinations of the blood and urine for hormones, examination of the blood and urine for vitamins and virological examinations, etc., as well as good illustrations have been added.

Many new methods are included, although none of the approved methods previously described have been omitted. Among the new methods given, to mention only a few, are the newer simplified methods for the cultivation and identification of anaerobic bacteria, methods for detecting the Rh subgroup in relation to blood transfusion, methods for testing the susceptibility of bacteria to penicillin and for the demonstration of penicillin in the blood, exudates, and other body fluids, methods of detecting and identifying the crystals of the sulfonamide compounds in urine, etc.

The bacteriological nomenclature followed in general is out of date. Diphtheria bacilli for example are referred to as *B. diphtheriae*, with the correct or at least now most commonly accepted "Bergy" terminology *Corynebacterium bacterium* given only once and then in parenthesis. This will be very confusing to recent graduates who have been taught the Bergy classification.

The format is new and condensed. The index is good, and the omission of numbered chapters and sections is not confusing. This book certainly ranks very high in its field and is one of the most practical and most widely used reference books in most clinical and public health laboratories. It is very gratifying to know that a Spanish language edition is in preparation.

Elizabeth Petran

The Pacific Islands Handbook 1944. *North American Edition.*

By R. W. Robson. The Macmillan Company, New York. $4.00. xii + 371 pp.; 4 maps. 1945.

This is a surprisingly readable collection of factual material on the Pacific Island world. The readability comes from two sources: the author is a lifelong newspaper man, and he has included much more historical material than it is customary to find in a handbook.

There are many maps of the islands. Data are given on population, government, geography, economics, etc., varying somewhat from island to island, apparently depending upon the amount and type of material available.

If one of the virtues of the book is its enjoyable journalistic style, one must also record that the opening sections, where the war in the Pacific is chronicled, seem too luridly journalistic. Such phrases as "horrible enemy," "our children guarded against the stealthy, creeping treachery of a race so different from our own that it might have come from another planet," seem out of place in scholarly writing.

George F. Carter

Carnegie Institution of Washington Year Book Number 43. *July 1, 1943—June 30, 1944, With Administrative Reports through December 15, 1944.*

Carnegie Institution of Washington, Washington, D. C. $1.50 (cloth); $1.00 (paper). xxxiv + 206 pp. 1944.

In addition to the reports of the Executive Committee and of the President of the Carnegie Institution, the Year Book always includes summaries of the research of the Institution's various departments. Biologists have long recognized these reports as having considerable value, since they frequently include preliminary results of researches still in progress, often some years ahead of final publication. Sometimes, too, there are items of special interest that never find their way into other print. The present volume is no exception.

The Division of Plant Biology reports, for example, work on the antibiotic chlorellin and extensive studies on *Poa* and other forage grasses, the latter undertaken to secure, through hybridization and polyploidy, superior types for restocking the Western ranges. New very early human embryos, effects of hormones on the differentiation on the sexual organs of the opossum, and other studies on the sex hormones are reported by the Department of Embryology. There is also a very interesting summary of work on the transfer of substances through the placenta, using heavy water and radioactive sodium as tracers. Report of a sarcoma-producing extract and of a tissue-cultured rhabdomyoma are also worth special notice. The Department of Genetics contributes much the lengthiest report on biological subjects, including: bacteriophage- or ultraviolet-resistant mutants of *E. coli*, penicillin-resistant mutants of *Staph. aureus*, radiation experiments with *Neurospora* and *Penicillium*, and mutations of bacteriophage; extensive studies of the distribution of chromosome breaks in *Drosophila*; mitosis in corneas of rats and rabbits; the genetic structure of natural populations, including studies of frequency changes of chromosome types in artificial populations and of sexual isolation between South and Central American strains of several *Drosophila* species; deficiency mutants and directed mutation in maize; polyploidy in *T. kok-saghyz*; the successful breeding of a low-marihuana strain of hemp; a new type of sex chromosome balance in hemp; longevity and foster-nursing in relation to mouse leukemia; and a considerable section embodying the last report on endocrine studies by Oscar Riddle, retiring as investigator this year after a long and productive service with the Carnegie Institution. Perusal of these reports, far better than examination of the financial statement, affords a measure of the great contribution of the Carnegie Institution to American science.

BENTLEY GLASS

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